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A. Guayule field with all plants above 40 cm. removed. Lomas of Sierra Zuluaga.  
 B. Guayule field of maximum density, near Apizolaya.



# GUAYULE

(PARTHENIUM ARGENTATUM GRAY)

## A RUBBER-PLANT OF THE CHIHUAHUAN DESERT

BY

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## PREFACE.

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In 1907 the author of the present paper was engaged by the Continental-Mexican Rubber Company and the Intercontinental Rubber Company to organize investigations looking toward the successful cultivation of a Mexican desert rubber plant, the guayule (*Parthenium argentatum* Gray). Dr. Theodore Whittelsey and Dr. J. E. Kirkwood later became identified with this undertaking, the former as chemist, the latter as assistant botanist. The headquarters for the investigations were established at the Hacienda de Cedros, Partido de Mazapil, Zacatecas, Mexico. It was not a matter for congratulation that, at the close of a year, the directors found it inadvisable, for financial reasons consequent on the panic of 1907, to continue the department of investigation. By the courtesy of the company, however, the author carried on his studies for some three months beyond the termination of his business relations with it, and this period, falling during the growing season of 1908, brought to light many important facts. Still further observations of capital importance, in part on experiments begun in 1907 and 1908, were made by the writer in April 1909, while representing the United States Rubber Company, a commission which could not have been prosecuted without the kind concurrence of President C. C. Thach and a number of the writer's colleagues at the Alabama Polytechnic Institute. As silence was not imposed by the United States Rubber Company, it has been possible to include these observations.

No less than hearty recognition is due also to Mr. W. H. Stayton, formerly captain, U. S. Navy, sometime president of the Continental-Mexican Rubber Company, and now president of the Texas Rubber Company. It is stating an open secret to say that it was through the initiative and enthusiasm of this gentleman that the work of the investigation was undertaken and would have been continued but for circumstances beyond his control. Mr. Stayton has shown a liberal and scientific spirit, qualities not of necessity nor at all times associated.

Thanks are due further to Prof. J. C. Arthur and Prof. W. G. Farlow for reports on various pathological matters; to Dr. M. T. Cook for contributing manuscript on the galls found on guayule; to Dr. A. D. Hopkins for a report on the guayule bark-borer; to Dr. L. O. Howard and Dr. J. G. Sanders for the identification of certain insects; and to Prof. B. L. Robinson for his courtesy in causing a photograph of the type specimen of guayule to be made. Mr. Charles S. Ridgway has rendered substantial aid in the preparation of certain figures.

The drawing for figure 5 was supplied by Professor Arthur; the negative of plate 2, fig. B, was made by Dr. W. E. Hinds; Professor Trelease furnished the illustration (fig. 4) and description of the Cedros sotol, and kindly made several other determinations; the negatives of plate 3 and

plate 4, fig. A, were made by Mr. Victor Blanco. Dr. H. van der Linde obtained for me valuable material of irrigated plants from Caopas.

Dr. Theo. Holm has afforded me the benefit of his criticism of the portion of this work treating of the anatomy, and has been good enough to examine inaccessible literature for me. Dr. W. E. Safford did a like service regarding a few pages in the first chapter.

To Prof. W. L. Bray I am indebted for information about the Texas guayule fields, later verified by me personally; and to my colleagues, Prof. C. L. Hare and Prof. J. P. C. Southall, for assistance in making chemical analyses and for mathematical formulæ, respectively.

With reference to the chapters which follow, no pretensions are made with regard to completeness. The exhaustive study of a single plant from all points of view might well be numbered among the labors of fable. The reader is asked also to remember that the study of but a single growing-period was possible. Much of the experimentation, therefore, was done, as it eventually turned out, during the most unfavorable season; but in the case of field experiments this was not entirely a misfortune. That the theoretical bearing of many observations and more refined methods of making them are less attended to than the matter warrants has been due to the urgent necessity of practical success. With these qualifications, the work may be regarded as a report on a unique opportunity, unhappily shortly terminated, to bring a hitherto feral desert plant under the subjugation of culture. That success may ultimately be attained is not an unreasonable nor an unwarranted expectation, for which statement the interested reader will find not a little evidence in what follows.

FRANCIS ERNEST LLOYD.

ALABAMA POLYTECHNIC INSTITUTE,  
*January 1910.*



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GUAYULE (PARTHENIUM ARGENTATUM GRAY):  
A RUBBER PLANT OF THE CHIHUAHUAN DESERT.

By  
FRANCIS ERNEST LLOYD,  
Professor of Plant Physiology, Alabama Polytechnic Institute.

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# CHAPTER I.

## HISTORICAL ACCOUNT.

Since about the middle of the last century, after the epoch-making discovery of Charles Goodyear was made, the demand for crude rubber has been steadily increasing. This demand was for a long period satisfied by the products harvested from the tropical forests of the Old and New Worlds by natives whose methods are resulting in a gradual depletion of the natural supply. This, in turn, has stimulated research in three directions: toward obtaining a synthetic rubber, the ambition of the chemist; toward discovering other rubber-producing plants, for which search has been made into the farthest reaches of the tropical forests of the world; and, finally, in the direction of the culture of the various plants which before had been, in their feral condition, the source of the much-desired material. Whatever the promise of the chemist may be, there appears to be no abatement of interest at present in the culture of those better-known trees which have been found to adapt themselves to the hand of man, or in the discovery of hitherto unknown rubber plants. Each new announcement, however vague the authority may be, that a new rubber plant has been found, is hailed with precipitous interest; and one that is well founded is soon followed by a period of exploitation scarcely less fevered than on the finding of new gold-bearing fields. When, a very few years ago, it became more generally known that the plant commonly known as the guayule, and containing an economically valuable amount of rubber, grew in abundance in the desert country of northern Mexico, the vegetation of the adjacent arid areas underwent minute examination in the hope of finding either this or other similarly valuable plants, and even at the present moment the excitement has not died away.

The mere fact, however, that a plant indigenous to the desert should be found to be of enough value to set in motion large business operations involving millions of capital, based on the amount of the raw material in sight, is sufficient to awaken definite interest. The economic value of the desert is changed, and possibilities for the development of wealth in a supposedly barren country take on new dimensions. This has occurred, in point of fact, as a direct result of the discovery that the plant guayule produces in the neighborhood of 10 per cent of its weight of "bone-dry" marketable rubber. With the economic history, bionomics, structure, and micro-chemistry of this plant the present essay has to deal.

### ORIGINAL DISCOVERY AND DESCRIPTION.

The guayule was first discovered by J. M. Bigelow, M.D., in 1852, while attached to the Mexican Boundary Survey, "near Escondido Creek, Texas." It was first described by Professor Asa Gray some years later. His original description was based upon the type specimen, which is now

in the Gray Herbarium of Harvard University. A reproduction of this specimen is here given (plate 2, fig. A). The name in the right-hand corner is in the writing of Professor Gray. The label is Bigelow's field label. Following is the description published in the "Botany of the Boundary," p. 86, 1859:

*Parthenium argentatum* (sp. nov.): fruticosum, pube brevi appressima sericeo-incanum; foliis spathulato-lanceolatis oblongisve in petiolum longe attenuatis parce dentatis seu laciniatis sub-triplinerviis; ramulis floridis elongatis nudis oligocephalis; involucri squamis obtusissimis; acheniis sericeis; pappo e paleis 2 membranaceis lanceolatis.—Near Escondido Creek, Texas, in rocky places, Sept., 1852; Dr. Bigelow.—A well-marked species, connecting the sections *Argyrochæta* and *Parthenichæta*; the leaves and branches whitened with a very fine and close silk-silvery pubescence, which appears to be wholly or nearly persistent. Leaves one to two inches long, including the tapering base and petiole; 2 to 5 lines wide, mostly acute, scarcely veined, beset on each margin with from one to three salient teeth, or sharp lobes. Flowering branchlets slender, 4 to 8 inches long, nearly leafless and peduncle-like, bearing 3 to 7 sub-sessile heads (as large as those of *P. incanum*) in a cluster. Exterior scales of the involucre short, orbicular-ovate; the inner orbicular, scarious-membranaceous. Paleæ of the pappus lanceolate or oblong-lanceolate, rather narrower and less obtuse than in *P. hystero-phorus*, puberulent, the inner edge more or less adnate to the base of the broadly obovate and cucullate emarginate ligule.<sup>1</sup> (Fig. 9.)

As will be seen, the crowding of the heads to form a "cluster" depends upon external conditions. In a later description published by Gray in the "Synoptical Flora,"<sup>2</sup> we find the first hint of the peculiarity which later brought it into economic prominence. This description is as follows:

*P. argentatum* Gray. Suffrutescent, a foot high, silvery-canescient with close tomentum; branches erect, rather leafless above, bearing comparatively large and few heads (of 2 lines in diameter); leaves lanceolate to spatulate in outline, some entire or incisely 2-3 toothed, the larger incisely pinnatifid into 2 to 7 acute lateral lobes; pappus a pair of lanceolate chaffy awns (Bot. Mex. Bound., 86; Southwest border of Texas, Bigelow; Adj. Mex., Parry, Palmer; produces a gum or resin in Mexico).

### THE VULGAR NAME.

The name<sup>3</sup> "guayule" is properly applied only to *Parthenium argentatum* Gray. On account, however, of a superficial resemblance it has to certain other plants, especially because of similarities in size and in the gray color (so often seen in the desert) of the foliage, these have been wrongly called by the same name.<sup>4</sup> The mariola (*P. incanum* H. B. K., plate 44, fig. B), a closely related species, is one of these; and its very general association with the guayule proper has led to much error in estimating acreage of guayule. It is of interest in this connection to note that the mariola is known to the peon, in some parts at any rate, as "hembra de guayule,"<sup>5</sup> apparently because of the very constant associ-

<sup>1</sup> Gray, in Torrey, Botany of the Boundary, U. S. and Mex. Boundary Surv., p. 86, 1859.

<sup>2</sup> Synoptical Flora of North America, vol. 1, pt. 2, p. 245, 1886.

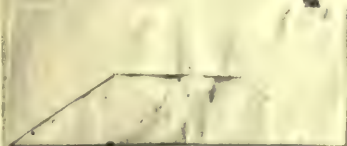
<sup>3</sup> Investigated by Endlich, 1905.

<sup>4</sup> The name is also applied to *Crysactinia mexicana* Gray, and more recently also to *Euphorbia misera*, material of which was sent to Dr. J. N. Rose, of the U. S. National Herbarium, from southern California, on the supposition that it contained rubber.

<sup>5</sup> The female guayule.



A



No. 83

Parthenium

near Escondido Creek,  
Mexico Sept. 1852

B



SYN. FL. N. AMER.

*Parthenium argentatum*  
Gray

A. The type specimen of *Parthenium argentatum* Gray.  
B. Transverse section of a very old stem.



ation of the two species, and because of the belief that this association is in some way necessary to the production of seed. Other species of the genus, some of which are annuals, have also received the name guayule, while a plant of the Sonoran Desert (Sonora and southern Arizona), *Encelia farinosa*, is not only mistaken to-day for guayule but is believed by many to contain rubber. The amount, if present at all, is so insignificant that it would certainly not repay consideration from a commercial point of view.

The guayule is known also as "yerba de hule" in the region of Pasaje, Durango, and simply as "hule" in some parts of Zacatecas and of Chihuahua. An alternative spelling "yule" (which occurs incorrectly as "llule" in "guallule") is used in some parts of San Luis Potosi. The name xihuete<sup>1</sup> occurs in northern Zacatecas and "about Saltillo"; copallin and afinador are other less-used designations. But the name "guayule" thus spelled is in the ascendant and will in all probability replace other names. Its derivation, in common with other Mexicanisms, has speculative interest. Seler<sup>2</sup> would refer it to *quahu* (wood, tree, or forest) and *olli* (rubber, Sp. *hule*), evidently believing it to be of Aztec origin. This etymology finds support in the aboriginal term *ulequahuatl*, said by Sahagún (1529) and Augustin Torquemada (1615) to be applied to a latex tree (probably *Castilloa*) producing *ulli*, a dark resin which becomes very elastic (Jumelle, 1903). By inversion, we have *quahu* + *ule*. The suggestion that the derivation is from the Castilian *hay* (there is) and the Aztec *olli*, from which we therefore have *hayolli*, which becomes *hayule* and so guayule, can not be seriously entertained.

#### PRIMITIVE AND LATER USES.

Contact with the country peon of Mexico reveals a great deal of resourcefulness in the use of many plants. In out of the way places a game is played with a small, very resilient ball, not purchased in the market. It proves on examination to be of very pure rubber, obtained by communal mastication of the bark of the guayule. Altamirano (1906) tells us that country boys obtain rubber in a similar manner also from "tataniní," a name applied, in Querétaro, to *Parthenium incanum* and to *P. lyratum*. This custom dates back with fair certainty to the middle of the eighteenth century, having been noted by a Jesuit, one Negrete.<sup>3</sup>

Mr. W. H. Stayton, formerly captain in the U. S. Navy, when on duty in the Gulf of California, observed the Yaqui Indians ashore playing a game with a ball about twice the diameter of a baseball. The game consisted in throwing the ball from hip to hip. It is not unlikely that the ball was made of guayule rubber, which could have been obtained from the country east of the Sierra Madre, or even of rubber from tataniní,

<sup>1</sup> From the Nahuatl *xihuatl*, weed. This spelling is given by Endlich (*loc. cit.*). "Jihuete" is given in Zacatecas. "Gihuete" occurs in a legal instrument drawn up at Matamoras, Coahuila, under date of March 9, 1905, in which also "hule" is given as designating guayule.

<sup>2</sup> Endlich, *loc. cit.*

<sup>3</sup> According to Juan Fritz, *vide* Endlich, 1906.



mariola, or other plant. The possibility that it came from the South is, however, not excluded. Peter Martyr (1569; published in 1830), Sahagún (1529), and Herrera (1492-1526) all speak of balls made of rubber made from latex trees.<sup>1</sup>

There can therefore be little doubt that, in common with the manufacture of mescal, extraction of fibers, and like primitive industries, the making of rubber balls from the guayule, just as from latex plants, antedates the invasion of Mexico by the Spaniard. It may be mentioned in passing that the method of extracting the rubber as above noted is analogous to the only widely used modern method of obtaining the crude rubber on a large scale, namely, by a purely mechanical process. The rationale of this will be seen beyond. In this connection a recent discovery of a piece of rubber which is undoubtedly of ancient origin on an old aboriginal village-site in Arizona is of peculiar interest. Of this discovery the following account is furnished me by Prof. R. H. Forbes:

The lump of rubber, a portion of which I recently handed you, was found in December (or thereabouts), 1909, at the west end of the Santa Cruz Reservoir and Land Company's dam, 14 miles west of Sasco, Ariz. Mr. C. O. Austin, who was present, states that this ball of rubber was contained in a small olla with articles of stone belonging to the *older* prehistoric ruins of this country. The find was made at about 3 feet below the general surface which was formed by the off-wash of an adjacent low mountain. No traces of houses on the present level of the land, according to Mr. Austin, were visible. One other ball of rubber was found here, and is now in Col. W. C. Greene's collection at Cananea. I regard this find as genuine, as Mr. Austin is familiar with Salt River Valley ruins and his statements are confirmed by others.

Microscopic examination of the specimen to which Professor Forbes refers throws doubt on the view that it is guayule rubber, but a final statement can not at present be made.

A record of this kind would be incomplete without reference to the use of guayule as a fuel. On account of its resin content, the plant burns with a fierce, smoky flame, after the fashion of "fat pine;" so that whenever it was available it was invariably used as a fuel for the crude Mexican adobe smelters, ruins of which are frequently seen in the mining districts. In this way thousands of acres have been depleted of their guayule, a wasteful process which was quickly stopped when the value of the plant became known. It can scarcely be doubted that many peculiarities of local distribution within restricted regions are due to the pulling of the guayule for fuel. Thus a large smelter and a number of roasting furnaces were in operation at Cedros,<sup>2</sup> the head fraction of the hacienda of that name lying to the west of Mazapil, for a term of years, and this circumstance is often referred to by the peons to explain the absence of guayule in places where it would naturally be expected. The case is analogous to the use of walnut for fuel and fence-rails in the early days in the eastern United States.

<sup>1</sup> Jumelle, 1903, quotes these authors at length.

<sup>2</sup> According to Juan Robles, whose duty it was, in 1856, to weigh the shrub as it came into the fundición at Cedros, guayule was paid for at the rate of 18 centavos per carga (6 arrobas=70 kilos), or about 17 pounds for 1 cent (gold)! The women on Cedros burned guayule in their bread ovens as late as 1894 (*vide* G. R. Fleming). Guayule shrub now fetches 150 pesos the ton.

## HISTORY OF MANUFACTURE.

Public attention was drawn to guayule rubber,<sup>1</sup> apparently for the first time in 1876, by an exhibition sent from Durango to the Centennial Exposition at Philadelphia (Pearson, 1907). In the same year, according to the Mexican Herald, the Natural History Society of Mexico took up the study of the plant and reported the presence of rubber of good quality (Delafond, 1908).

The first move toward the utilization of guayule rubber other than by the natives appears to have been made in 1888, when a company, the name of which is unknown to me, but probably the Mechanical Rubber Co., of Passaic, New Jersey, sent a special agent to Mexico with instructions to "obtain a large quantity" of "rubber-bark," "from which it was proposed to extract the rubber by a process of grinding and washing." According to the account, the agent seems not to have clearly understood his instructions, and shipped to New York 100,000 pounds of the entire shrub! The company in question did not relish paying the freight on the wood, and this item of expense deterred further investigation. However, the shrub was decorticated, the bark and twigs ground up finely, and "immersed in hot water \* \* \* finally coagulating the rubber into one mass." The result was an extraction of 18 per cent rubber (the wood of course not entering into the count), the quality of which was regarded as equal "to the best grade of Centrals," and a specimen was reported<sup>2</sup> to have been in good condition in 1895. There seems to be little doubt that the "rubber-bark" referred to in the preceding paragraph was guayule, though ignorance of the identification was confessed. However, the material was collected at Hot Springs (Aguas Calientes), Chihuahua, and was referred to in a letter by the local agent, who undertook the collection, as "hule."<sup>3</sup>

In this same year, 1888 or thereabout, a Mr. Herbert Wilson sent a sample of the rubber to England for analysis, and at about this time also Herr Juan Fritz employed a number of peons to chew out a sufficient amount of the raw material for examination, and this he sent for study to a German chemist, whose report was a practical condemnation of the rubber as an article of commerce.

Shipments of crude shrub made to Hamburg in 1900 were treated with caustic soda and small amounts of rubber thus recovered were placed on the market. In the following year 25 or 30 pounds of guayule rubber were sent to the market from a laboratory which had been established by Germans at San Luis Potosi. The earliest efforts seem to have centered here, so that San Luis Potosi may be regarded as the birthplace of the industry.

The laboratory experience at San Luis Potosi led in 1902 to the establishment of a factory at Jimulco, by Adolf Marx, representing the

<sup>1</sup> I have been unable to obtain a transcript from the original records. An anonymous writer in the India Rubber World, April 10, 1895, refers to this exhibit as rubber from "a native plant of the genus *Cynanchum*, of the natural order Asclepiadaceæ, according to Mr. Fernando Altamirano."

<sup>2</sup> In the India Rubber World, 10: April, 1895: "Extraction of rubber from minor plants" (unsigned), upon which I base the account in this paragraph.

<sup>3</sup> India Rubber World, *loc. cit.*



Compañía Explotadora de Caucho Mexicano, from which factory rubber was put on the market for the first time in 1905. In 1902, also, certain American capitalists financed an expensive but eventually successful series of experiments which led to the successful extraction of the crude rubber by a mechanical process (devised by Mr. Wm. A. Lawrence), and two years later, in 1904, the first lot of rubber thus prepared was taken by the Manhattan Rubber Company. On December 25, 1904, 50 pounds of crude rubber, extracted by means of the now successfully adapted pebble-mill, were shipped to the United States, over half of the amount being purchased by the Manhattan Rubber Company. Then followed the building of a large factory at Torreón by the Continental-Mexican Rubber Company (plate 3, plate 4, fig. A), in which the results of the earlier experiments were used. This event marked the beginning of commercial success in the extraction of rubber from the guayule shrub by the mechanical method, which has superseded all others, and it should be said that this phase in the development of the industry is almost entirely due to American initiative and ingenuity.

From 1905 on a large advance in the outlay of capital followed, and extracting plants of various sizes were established in San Luis Potosi, Saltillo, Monterey, and Gomez Palacio, as well as at Torreón and Jimulco.

Manufacturing enterprise has lately brought the guayule industry into Texas. On September 1, 1909, a factory<sup>1</sup> at Marathon, Texas, in the heart of the guayule area of that State, began operations under the Texas Rubber Company. But it should be added that the manufacture of guayule rubber had already to some extent been carried on in the United States and abroad. The extent of this phase of the industry is indicated in the total exportation of crude shrub from Mexico, the statistics for which are given on p. 11.<sup>2</sup>

At the present writing, according to Mr. Henry C. Pearson,<sup>3</sup> the outlay of American capital alone in Mexico amounts to \$30,000,000.

## METHODS OF EXTRACTION.

A brief statement of the principal features in the methods of extraction of rubber from guayule will be of interest here, especially as they differ widely from nearly all hitherto-used methods of preparing crude rubber from latex plants.<sup>4</sup> It must be understood that the rationale of the processes lies in the fact that the rubber exists as such in the cells of the plant, and will not escape by bleeding.

The material must, then, either be dissolved out, after preliminary grinding, by suitable chemical agents, or must be agglomerated mechanically, either with or without the assistance of a substance (caustic soda) which will attack the cell wall. The chemical method is used successfully, it is understood, at Akron, Ohio, where an excellent brand of guayule

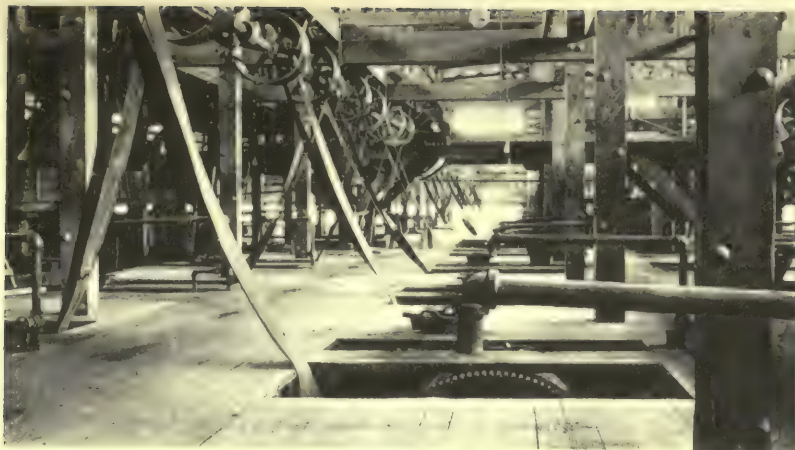
<sup>1</sup> Previously built and operated for a short time by the Big Bend Rubber Co.

<sup>2</sup> We now read that the Japanese have entered the market, and are buying shrub (Dec., 1909).

<sup>3</sup> India Rubber World, 40 : 383, August 1, 1909.

<sup>4</sup> African "grass-rubber," however, is obtained in a crude way, but purely mechanically, from species of *Landolphia* (Jumelle, 1903).

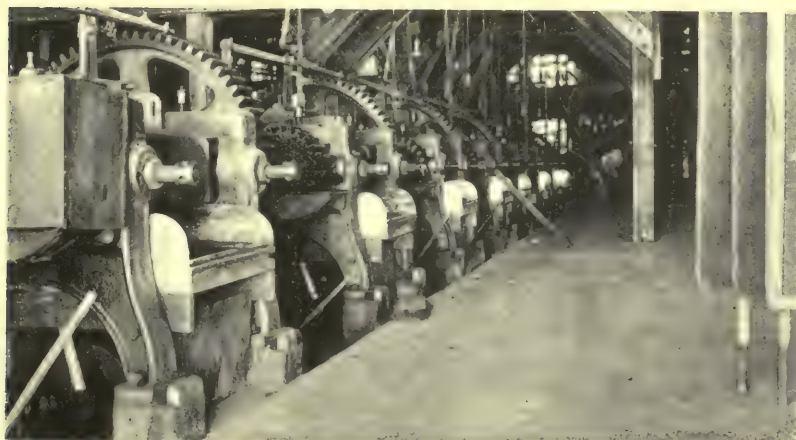




A



B



C

- A. Upper floor in a guayule factory from which pebble mills are charged.  
B. Lower floor: discharge chutes and ditch from pebble mills.  
C. A battery of washing and sheeting machines.





A



B

A. Stacks of guayule in bales. Continental-Mexican Rubber Co.

B. Experimental ground, with plants two years old, from stocks. Cedros.





rubber is produced. Although the principles involved are well known, the precise steps are preserved secret. The process, which is based on methods of organic analysis, is not widely used, and only a small part of the total manufacture is carried on in this way.

Of greater interest, not only in itself, but for the future economic development of the rubber industry, is the mechanical method. This may be described only in its broader outlines, since the steps employed by various manufacturers are changed from time to time as experience indicates.

The shrub is first washed so as to free it from dust and other foreign matters which affect the specific gravity of the "worm" rubber by becoming attached to the agglomerated particles. It is then passed between rolls which comminute it while it is being sprinkled with water.<sup>1</sup> The rolls used have been supplied with knives, or have been adapted to pulverize the material, or, as now used, the shrub may be run twice between corrugated rollers, running differentially, for the sake of even and fairly fine grinding. The resulting mass is then placed in a pebble-mill, which is a short cylinder of steel, lined with Belgian flint bricks, such as is used for grinding cement, paint, charcoal, and the like (plate 3, figs. A, B). The grinding is accomplished by means of Norwegian or Mediterranean flint shore-pebbles.<sup>2</sup>

The pebble-mill charge consists of one-third its volume of pebbles, one-half of water, together with 6 to 8 bushels of shrub. The mill is revolved at the rate of about 30 times a minute for a period lasting 90 minutes to 2 hours, at the expiration of which time there results a finely ground pulp consisting of minute agglomerations of rubber mixed with fine particles of bagasse. This is separated from the dirty water in which it was ground and is then run into tanks, where a skimming process separates the rubber, which floats, from the bagasse, which sinks. A part of the bagasse, however, does not sink at this time, namely, that consisting of flakes of light yellow cork.

Nor is the rubber free from particles of wood fiber, imprisoning more or less air, and this interferes with the complete separation of rubber and bagasse. The complete water-logging of the bagasse may be attained by means of a compressor, in which the skimmed rubber, with its adherent fiber, is subjected under water to a pressure of about 225 pounds for a period of 15 minutes to 2 hours, according to the kind of shrub being treated. Subsequent treatment in a beater-washer, an elliptical tank, supplied with a paddle-wheel of half its transverse diameter, prepares for the final separation of rubber and bagasse in settling-tanks.

<sup>1</sup> It has been suggested (Whittelsey, 1908) that decortication, previous to grinding, would be an economy. It is interesting to recall that this was done—on an experimental scale, albeit a generous one—in 1895 (India Rubber World, April 1895).

An alternative method, recently proposed by Chute and Randel (India Rubber World, vol. 42, p. 360, 1910), consists in grinding the shrub dry and then deresinating (the solvent to be recovered by distillation). The ground shrub, now supposedly free from resin, is then treated as here described, beginning with the pebble-mill.

<sup>2</sup> The internal structure of this mill has been the subject of numerous patents. Thus, steel balls, associated with various forms of projections from the interior surface of the cylinder, have been used, but without supplanting the "pebble-mill."

An alternative treatment consists in allowing the washed rubber from the first skimming-tank following the pebble-mill to soak for a week in settling-tanks, during which time the bagasse becomes water-logged and sinks. The soaking is probably of value also in separating from the rubber certain substances, probably enzymatic in character, which otherwise would contribute to the earlier breaking down of the rubber.

The clean rubber is now passed between corrugated and smooth rolls for the purpose of washing and sheeting (plate 3, fig. C), when the product is ready to be put on the market. Unless further treatment ensues, the rubber thus prepared contains about 25 per cent moisture, together with a proportion of resin.<sup>1</sup>

Other special steps in treatment are applied to the separation of rubber from bagasse, or in preparing special grades. For example, boiling the skimmed rubber in a 1 to 2 per cent solution of caustic soda has been used as an aid in the separation of rubber and fiber, and for partial deresination by the saponification of the resin acids. By this means the amount of resin, 25 per cent, usually present, may be reduced to 17 or 18 per cent.<sup>2</sup> Other modifications in treatment are necessitated by the condition of the plants when treatment is begun. Old, weathered and dried-out shrub is not worked with the same ease nor with the same result as fresh, while a certain amount of seasoning is an advantage. Considerable losses have been entailed by storing guayule in the yard exposed to the sun (plate 4, fig. A), as may be imagined if a million dollars' worth of shrub is handled in this way, even though the amount of deterioration is small. This loss is now avoided by placing the shrub in storehouses.

### THE NATURAL SUPPLY OF SHRUB.

With such large interests at stake, it soon became a matter of moment to determine the relation of supply of the shrub to the manufacture, as to total supply in sight, as to its rate of reproduction under natural conditions, and as to the possibility of its cultivation.

The first of these questions was naturally the first to be raised, and many attempts have presumably been made to find an answer. The earliest, and, so far as I am aware, the only published calculation was made by Endlich (*loc. cit.*), who assumed an average amount of half a ton per hectare in virgin fields. The total area of the general guayule region being taken as 75,000 square kilometers, and assuming that only one-tenth of this carries the shrub, Endlich arrived at the sum of 375,000 tons total supply in Mexico, which, at the rate of 7 to 10 per cent of rubber, represents 26,250 to 37,500 tons of rubber. This estimate was probably quite conservative, as indicated by calculations based upon official reports brought together in the *India Rubber World*.

Using the probable corrections for exports of crude rubber other than guayule, this publication gives the total imports of guayule rubber

<sup>1</sup> Whittelsey, 1909.

<sup>2</sup> At this writing an announcement is made (*Guayule Rubber by a New Process*, *India Rubber World*, December, 1909) that a method ("physico-mechanical"—*sic.*) has been patented whereby crude rubber, after treatment, has the composition: "Pure caoutchouc, 88 per cent; resin, 7 per cent; water, 5 per cent."



into the United States from June 30, 1905, to June 30, 1909, as 32,010,820 pounds. This being about 80 per cent of the total export, using the data for 1906-1908<sup>1</sup> as a basis, we have a total exportation of crude guayule rubber for four years of 40,013,525 pounds, which amount to 20,000 long tons in round numbers, representing, on the basis of 7 per cent extraction of rubber with 25 per cent moisture (5.25 per cent dry rubber), shrub, 286,000 tons; and on the basis of 15 per cent extraction of rubber with 25 per cent moisture (11.25 per cent dry rubber), shrub, 132,000 tons.

The last two sums give us the highly probable extremes between which the tonnage of shrub represented by crude-rubber exports falls. To the amount must be added the amount of shrub exported, for which figures for two and a half years are available, namely, 2745 tons. We have, therefore, the limits of 288,745 tons and 134,745 tons.

That the larger amount of shrub is nearer the true amount taken appears to be the case, since the extraction of rubber with 25 per cent moisture has only recently reached 15 per cent, and this is probably not attained by manufacturers in general. For a long time it fell below 10 per cent, so that an average extraction of 8 to 10 per cent of rubber (25 per cent moisture) is probably near the truth. This would represent, on the 8 per cent basis, 252,745 tons shrub; on the 10 per cent basis, 202,745 tons shrub.

It is therefore probable that in the neighborhood of 225,000 tons of shrub were disposed of up to June 1909. This, according to Endlich, would be somewhat over half the total original available supply. This estimate agrees with that of some interested informed persons who hold that one-half of the original supply is used. But estimates carefully made for business purposes show that there were at this time at least 200,000 tons still available. Of this amount, I myself have seen at least 100,000 tons in a comparatively restricted area on three estates.

Allowing for guayule still remaining on fields which have been gone over, and which in certain well-known cases is in considerable amount, it seems not improbable that the total original amount reached 500,000 tons. The amount in Texas in the Big Bend country is not known and must therefore be left out of account, but without it it does not seem probable that the total amount of virgin shrub is sufficient to last more than four to six years at the present rate of consumption.<sup>2</sup> It is likely that the smaller concerns will be closed out, so that, with a reasonably restricted output, the supply may be made to last six to eight years, which is the period during which the solution of the cultivation of the plant must be compassed if it is to keep the industry on its feet.

<sup>1</sup> India Rubber World, September 1909. For 1906 to 1908 the total crude rubber exports were 22,693,489 pounds, while our total imports were 17,917,342 pounds.

<sup>2</sup> The recent high prices paid for crude rubbers have stimulated the manufacture of guayule rubber, which has brought as much as \$1.25 per pound. The imports into the United States for the year ending June 1910 were, approximately, 10,000 long tons. On the basis stated above, this quantity represents something between 66,000 and 145,000 tons of shrub, but, in view of the improved methods, the smaller figure lies nearer the truth. If we assume a 12 per cent extraction, we get 83,300 tons of shrub used in the year.

As in all commercial enterprises depending upon the rate of growth of the raw material, and more notably of lumber trees, the methods were and still are conducted without relation to the future. When, however, the capitalist began to see that nature had set a definite limit to the rate of supply, it became a matter of moment to determine what could be done to meet the demand. The method of obtaining the shrub, when not owned outright, is by contract between the companies and the hacendados whose lands support a growth of the desired plant. These gentlemen at first signed contracts at a very low figure, but when they saw the market stiffen and their acreage continually reduced, they very naturally began to take thought for the morrow. I have conversed with hacendados who had for some years endeavored to germinate the seed, in the hope of solving the problem of cultivating the plant. Lack of success, however, was the chief result of such effort, though a few doubtless succeeded in getting plants to grow. Indeed, optimistic statements as to the possibility of growing the plant profitably have been made in some quarters,<sup>1</sup> and it has even been claimed that the whole problem of cultivation at a profit has been solved. As will be seen, however, in what follows, as regards the secretion of rubber, which is the all-important point, a very great deal of caution should, in view of the lack of evidence, have qualified any statement of this kind. It seems more consonant with the truth, as well as with business methods (a not invidious juxtaposition, it is hoped), to take a skeptical attitude, which, however, need not be unduly pessimistic. It is rash at best to attempt to foretell what solution science may bring to any problem.

#### ATTEMPTS AT CULTURE.

That hope has been entertained that the cultivation of guayule on a profitable basis may be possible is evident. In addition to private owners, at least two companies have spent time and money in seeking this end, if unauthoritative statements may be relied upon. Of these the Continental-Mexican Rubber Company essayed to make a serious trial, and employed a scientific corps to undertake research looking to the final solution of the question.<sup>2</sup>

It is not surprising that so valuable a desert plant should have attracted the attention of interested persons of other nations whose authority extends over desert areas in other parts of the world. No detailed statement on this score can be made, however, beyond that the Germans<sup>3</sup> are said to be conducting experiments in the cultivation of guayule in East Africa. The feeling properly exists that any effort toward the subjugation of the desert is justified. The time will come when not only those parts of arid regions which may be brought under irrigation, but those also which remain unmodified in this regard, will yield their possibilities to the hand of man, and we stand at this moment at the serious beginning of this conquest.

<sup>1</sup> See *India Rubber World*, May 1, 1908.

<sup>2</sup> This work has recently been taken up anew (September 1910).

<sup>3</sup> Ross, 1908.

## CHAPTER II.

### THE ENVIRONMENT.

#### GEOGRAPHICAL DISTRIBUTION.

The northern limit of distribution of the guayule is in the southwestern part of Texas, where it occurs in Presidio, Brewster, and Pecos (near Langtry) Counties. This area is continuous with its area of distribution in Mexico, throughout which it occurs with greater or less frequency. The periphery of this area runs approximately as follows: from the western extremity of Presidio County in Texas, the western boundary will run somewhat west of south till it reaches the northern boundary of Durango, near Santa Barbara, Chihuahua.<sup>1</sup> From this point the limit turns approximately toward the southeast, running parallel with the Mexican Central Railway at a distance of about 100 kilometers (Endlich, 1905). Beyond the state of Durango the boundary turns still farther to the east, curving northward again not far from the city of San Luis Potosi.<sup>2</sup> The 101st meridian marks roughly the eastern boundary, lying somewhat west of it till beyond Saltillo, where the boundary then curves slightly west of north, reaching the eastern limit in Texas at about Langtry. The northern limit is marked approximately by Fort Stockton.

The guayule is thus seen to be peculiar to the Chihuahuan desert. The belief which has sometimes been entertained that it occurs in western Sonora, southern Arizona, and New Mexico seems not to be well founded, and the area within which it is found is confined to the northern portion of the central plateau, embracing an area of approximately 130,000 square miles, or 290,000 square kilometers. Of this area, it will be understood that only a small proportion will be found to carry guayule, and a rough estimate of 10 per cent would certainly not be too low. Endlich's (1905) estimate, 75,000 square kilometers, is probably as nearly correct as we may make it. It may here be remarked that the very great irregularity of distribution makes it very difficult indeed to make anything approaching an accurate estimate of the amount of guayule as to acreage alone, aside from the question of density, so that any figures which may be given are subject to correction.

#### ALTITUDINAL DISTRIBUTION.

The whole region in question is, as already said, embraced within the northern part of the central plateau (mesa central) of Mexico and the adjacent area within which guayule is found in Texas. This area has an altitude varying from 2,000 to 10,000 feet above sea-level. The

<sup>1</sup> Mr. W. H. Stayton reports seeing a small amount of guayule in the Sierra Madre east of Sahuaripa, Sonora. The amount on the eastern slope was somewhat greater than on the western. It is now believed to occur sparingly in eastern Sonora.

<sup>2</sup> I am informed that Pringle found guayule near Pachuca, Hidalgo, which is probably its southernmost limit.



range of the plant in altitude extends from the lower limit mentioned to about 7,000 feet, or somewhat higher. As observed by Endlich (1905), however, the most important acreage is not usually to be found much above 6,000 or 6,500 feet.

#### CLIMATE.

The climatic conditions under which the guayule lives have not only scientific interest, but very important practical bearings as well. This will be understood upon the reflection that many proposed operations relative to the culture of the plant involve the use of water, and whatever the theoretical possibilities may be, success on a large scale must be conditioned very closely by the nature of the desert areas to be utilized. The details in question will be considered in Chapters VIII and IX. For these reasons a somewhat detailed account of the actual climatic conditions observed at Cedros, in North Zacatecas, will be given.

#### RAINFALL.

Fortunately, perhaps, for our purposes, the year (1907-08) during which observations were begun was unusually dry, and afforded, we believe, about the most rigorous conditions which the vegetation is subjected to without marked unfavorable results. It is to be regretted that data for the whole of this year can not be reported, since observations could not be commenced before the month of August. Relying upon estimates and upon general, verbal reports, and judging by analogy with the region about the city of Zacatecas, where the precipitation for 1907 was about half (320 mm.) of the mean for 29 years (596 mm.),<sup>1</sup> it seems reasonable to believe that the total rainfall for 1907 was not greater than 175 mm. (7 inches), of which 138 mm. were recorded instrumentally as falling during the last four months. The growing season, as would be indicated by the scant amount of rain which fell earlier in the year, was a practical failure as regards crops in general, and the indications of growth in the guayule, which at this moment concern us most, were consonant with the precipitation, which was at best very scanty.

As will be seen upon examination of table 1 and fig. 3, the rainfall for 1908 was somewhat over 10 inches, which appears to be about normal, while the effective rains fall in the summer months. In 1908 it was sufficient to produce a prolonged period of relatively high atmospheric humidity, while the replenishment of the store of water in the soil was marked enough to produce very pronounced mesophytic conditions. In the low-lying flats, especially where the more abundant collections of water were formed, annual plants of weedy appearance grew densely breast-high, and seedlings of the mariola scattered among them grew with great rapidity to a height of 40 to 50 cm. in one season. On the low ridges and in the hills the available stratum of the soil was full of water, and the guayule and mariola, together with many other shrubs and annuals, were in full bloom and making rapid growth in June. Other features of the distribution of rains are indicated in a general way in the diagram and are of importance as related to the period of growth of the guayule, to be referred to beyond.

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<sup>1</sup> Boletín Mensual del Obs. Astron.-Meteor. Zacatecas, Jan. 21, 1908.

TABLE 1.—Rainfall at Cedros, September 1907 to August 1908 (fig. 3).

Date.	Millimeters.	Date.	Millimeters.	Date.	Millimeters.
1907		1908		1908	
Sept. 9	24.4	Mar. 9	trace	July 7	9.8
Oct. 4	68.3	15	trace	9	3.0
10	1.2	21	45.0	13	12.8
19	7.2	27	trace	14	24.0
Nov. 28	16.2	Apr. 3	9.4	20	5.8
Dec. 2	3.9	9	trace	21	3.4
9	7.8	11	7.0	22	trace
13	9.6	17	trace	27	4.8
		May 1	3.0	28	9.6
		18	3.6	29	trace
		27	6.0	30	trace
		30	16.8	31	8.4
1908		June 1	1.2	Aug. 1	4.5
Jan. 3	trace	4	2.4	6	3.0
18	trace	22	19.2	7	1.5
21	trace	23	14.4	12	5.0
26	trace	25	6.0	18	2.4
Feb. 1	trace			20	17.7
6	trace				

NOTE.—It seems probable that the rainfall for the four months of 1907 was relatively high, and includes an amount which normally would have been distributed earlier in the year, that is, in the summer months.

I visited Cedros during April 1909. Upon arrival there it was found that there had been no rain, save a few drops on a few occasions, between August 20, 1908, and April 5, 1909. On the latter date heavy showers occurred over considerable areas, leaving water standing in "charcos" for several days. This was a very persistent drought, and it was found to have affected guayule quite unfavorably in many localities. I am informed by Mr. G. R. Fleming that drought again persisted till June 16, 1909, when it was broken and a very abundant rainfall ensued during the summer of 1909.

#### AIR-TEMPERATURES.

Table 2 shows observed temperatures at Cedros during the time indicated. The lacunæ observable in May, June, July, and August are not as fatal to an adequate notion of the prevailing temperatures as might be supposed. A brief study of the table as a whole will show that the temperatures are remarkably uniform, and this is especially true of the months for which data are lacking. The readings, therefore, which were made nearly every day, were not recorded except as they showed variations of several degrees.

The lowest temperatures to which guayule may be subjected are not known. The minima at Cedros are undoubtedly higher than those which occur in the guayule region of Texas, but as meteorological data for that region are lacking we are compelled to judge by those of El Paso, the nearest station. The minimum temperatures observed here during the last twenty years range close to zero, so that we may infer that the guayule plant can withstand lower temperatures than those

encountered in North Zacatecas.<sup>1</sup> Attempts which may be made in the future in the cultivation of the plant, *e.g.*, in New Mexico, must be made with regard to its resistance to cold, and it is to be regretted, therefore, that a final datum on this point can not be given.

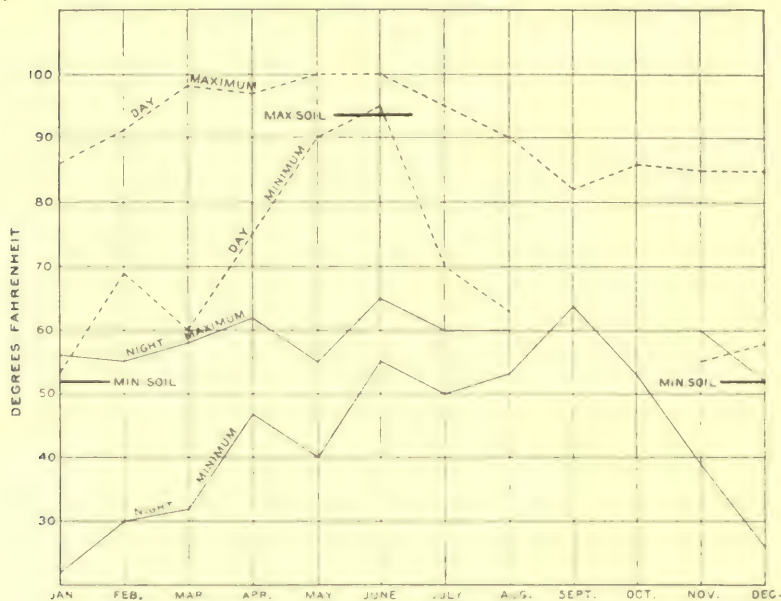


FIG. 1.—Maximum and minimum day and night temperatures by months; maximum summer and minimum winter soil-temperatures at 10 cm. depth. Cedros.

It will be noted upon examining fig. 1 that growing temperatures, though sometimes low, occur even during the winter months in the day-time. At night, however, the air-temperatures are seen to be practically non-effective between the middle of September and the beginning of May. This condition, judging from air-temperatures alone, may be regarded as resulting in a functional resting-period of at least three months; that is, the amount of growth possible in the year would be that occurring within nine months of time, aside from the consideration of rainfall. The soil-temperatures are of course higher, and are, on account of the high insolation, frequently favorable for the absorption of water by the roots, which would, under favorable conditions of soil-moisture, be important in respect to the water-content of the plant, though it might not, except when water was abundant or under otherwise exceptional conditions, stimulate growth. The conditions as regards growth, then, may be stated thus: The winter, or resting-period, is effective during the night-time chiefly during October and on to the end of April. The day temperatures during this period may effect growth when water is sufficient.

<sup>1</sup> We now have records showing that guayule can stand a temperature of 5° F. at Marathon, Texas, and of 10° F. at Tucson, Arizona.



TABLE 2.—Temperatures (in degrees Fahrenheit) observed at Cedros from November 1907 to August 1908.

Day of month.	Nov. 1907.		Dec. 1907.		Jan. 1908.		Feb. 1908.		March 1908.		April 1908.		May 1908.		June 1908.		July 1908.		August 1908.	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
1...	00	52	65	42	80	44	86	44	91	45	92	58	100	47	95	54	95	..	..	60
2...	82	52	70	41	78	46	75	42	92	47	90	55	90	..	100	65	..	60	..	60
3...	76	60	..	..	77	46	82	52	95	46	92	55	92	55	99	65	..	90	..	55
4...	74	44	61	41	81	44	87	52	90	48	88	50	..	..	..	..	..	..	..	..
5...	71	39	..	45	80	40	83	45	..	49	90	54	92	53	..	..	..	..	..	55
6...	74	40	58	41	68	36	73	43	92	52	94	62	..	..	..	62	95	..	..	..
7...	74	54	62	40	68	40	..	52	93	58	98	62	92	..	..	..	..	..	..	..
8...	84	45	67	40	68	35	80	36	98	53	..	58	..	..	..	..	..	..	..	..
9...	80	54	68	40	70	34	79	54	91	46	..	59	..	..	..	..	..	..	..	..
10...	85	50	..	32	68	22	86	53	82	43	84	49	90	50	..	..	..	..	..	..
11...	76	40	66	44	53	27	79	42	81	42	78	49	..	..	..	..	95	..	..	..
12...	62	40	..	45	64	27	82	50	88	50	75	..	..	..	..	..	..	..	..	..
13...	70	42	60	30	72	34	80	52	89	50	..	47	90	..	..	..	70	50	..	..
14...	76	40	70	36	72	26	73	30	91	51	86	57	..	..	..	..	..	..	..	..
15...	80	52	..	36	86	37	69	30	98	52	90	62	..	..	..	..	..	..	..	..
16...	78	46	72	46	78	40	78	40	90	50	94	..	..	..	..	..	..	..	..	..
17...	73	55	70	52	71	32	84	49	96	53	97	55	..	..	96	56	..	..	90	53
18...	80	56	72	52	68	35	81	45	92	53	90	60	..	..	96	56	..	..	63	57
19...	78	37	65	42	68	39	78	40	96	51	90	54	94	..	100	50	..	..	..	..
20...	70	50	70	50	..	46	79	40	96	56	86	56	..	..	95	56	70	50	..	..
21...	..	37	70	37	80	48	86	43	87	54	90	53	..	..	..	56	..	55	..	..
22...	..	35	57	26	79	40	90	42	84	46	..	55	..	..	..	..	50	55	..	..
23...	78	42	65	30	80	44	86	55	60	32	90	53	..	..	..	..	50	..	..	..
24...	..	55	60	32	79	39	91	42	70	42	..	52	..	..	..	55	..	..	..	..
25...	58	51	69	40	79	46	75	34	89	42	95	51	..	..	..	..	..	..	..	..
26...	..	55	80	44	84	48	81	41	88	55	92	50	40	..	..	..	..	..	..	..
27...	74	48	81	49	84	50	87	47	94	60	90	50	..	..	..	..	..	..	..	..
28...	..	46	85	52	85	..	84	46	94	60	90	52	..	..	..	..	..	..	..	..
29...	60	44	70	43	83	48	89	44	94	52	..	50	..	..	..	..	..	60	..	..
30...	55	42	84	45	85	56	..	..	95	60	92	49	95	54	..	..	65	53	..	..
31...	..	..	76	46	00	44	..	..	95	60	..	..	..	..	..	..	..	..	..	..

<sup>1</sup>First killing temperatures in cultivated areas.

TABLE 3.—Maximum and minimum temperatures at Cedros.

Month.	Max.	Min.	Mean.	Month.	Max.	Min.	Mean.
	°F.	°F.	°F.		°F.	°F.	°F.
Sept....	82	64	72	March...	98	32	71.4
Oct....	86	53	68	April....	97	47	71.9
Nov....	85	39	60	May....	100	40	74
Dec....	85	26	55.9	June....	100	55	75
Jan....	86.6	22.8	57.7	July....	95	50	72
Feb....	91	30	63.8	Aug....	90	53	67

## SOIL-TEMPERATURES.

A single record of soil-temperatures extending over a period of 15 months was made by means of a standard pair of thermometers. The instruments were buried at a depth of 10 cm.<sup>1</sup> below the surface of the ground at station 3. The surface had a gentle slope toward NE. by E.,

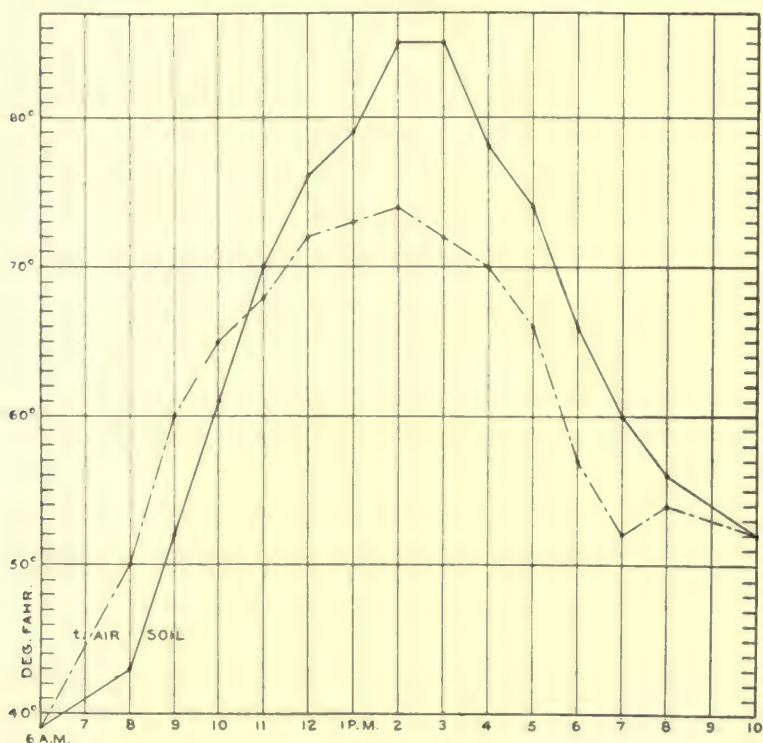


FIG. 2.—Air-temperatures (t.) and soil-temperatures at 2 cm. depth. November 6, 1907.

and would therefore receive neither the highest maximum nor the lowest minimum insolation. The indices stood at 70° F. when the instruments were buried, on December 31, 1907. They were removed April 2, 1909, when the following readings were taken: maximum temperature, 94° F.; minimum temperature, 52° F.

<sup>1</sup> This is about the average depth at which the lateral roots of the guayule are placed.

It is seen, therefore, that at the depth mentioned the lower critical growth temperatures in the soil are probably never reached, and it is to be inferred that the dormant condition of the vegetation is determined by other factors, namely, soil-moisture and air-temperatures, and of these the factor of moisture is probably the more effective.

The temperatures affecting germination, however, are those of the surface of the soil or at a very slight depth. Fig. 2 presents the curves of air and soil temperatures for November 6, 1907, at a time when difficulty, ultimately shown to be due to other causes than temperature, was experienced in germinating seeds in boxes. The soil-readings are for a depth of 2 cm., and the soil was wet, but was exposed to full insolation.

The temperatures from about 9 a.m. till 10 p.m. can not be said to be unfavorable, though their effect upon the rate of germination and subsequent growth would be offset by the succeeding hours of cool soil.<sup>1</sup> The cooler period is more marked during the succeeding months till March or April (fig. 1). Inasmuch, however, as the night temperatures are scarcely ever favorable for germination (assuming 40° Fahr. as the lower limit) before June or after October, and even during this period not especially so, we may conclude that the existing temperature conditions at Cedros are of subsidiary importance in determining the time of the year when germination occurs. This conclusion is supported by the success attending germination tests made in January (Kirkwood, 1910), when the temperatures ranged from 32° to 64° Fahr. At these temperatures, germination did not begin so soon as when, later on, they were somewhat higher. It therefore may be concluded that, aside from a certain rhythm which may be detected, winter dormancy both in the mature plant and in the seed is due, in the area we are considering, rather to lack of soil-moisture than to unfavorable soil-temperatures. This conclusion can not, however, be applied throughout the whole of the guayule region, since the winter temperatures in Texas are much more unfavorable.

#### SOIL-MOISTURE.

The residual soil-moisture during sustained periods of drought may be reduced to a point below the minimum necessary to sustain life. This is the chief cause of the local dying off of guayule during such periods. Generally, however, the amount of soil-moisture, though insufficient to stimulate growth even if other conditions are favorable, is more than enough to sustain life, and indeed may be enough for growth when the equilibrium between the plant and the environment is destroyed. The results of certain experiments detailed beyond show this to be true. Plants at station 2, quadrat 2, were pollarded in November 1907, about 5 to 8 cm. above the surface of the soil, and these had made a marked growth by February 18, 1908, although the surrounding plants showed no growth at all, and indeed did not until much later on. While there had been a very small amount of rain, it was quite insufficient to account for the growth, even in the pollarded plants, during the period between the dates above mentioned. We may therefore conclude that usually

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<sup>1</sup> Abbe, C., 1905, p. 36.



during dormant periods the soil-moisture is considerably above the necessary minimum,<sup>1</sup> but insufficient to stimulate to growth, although, on account of lack of facilities, a quantitative statement can not be made. This is to be regretted, because the peculiar distribution of the guayule in the foot-slope, while *Parthenium incanum* extends beyond its limits into the playa,<sup>2</sup> is probably connected either with the superior water-holding capacity of the soil of the foot-slope or with its greater air-content, aside from the differences observable in the topography of the root-systems of these plants. The naked statement that the guayule is confined to slopes which are well drained<sup>3</sup> conveys little of explanation.

#### RELATION OF RAINFALL AND TEMPERATURE TO GROWTH.

Whatever is said here about the behavior of the guayule in regard to growth-rhythm must be understood to apply to the region of North Zacatecas, where the data which appear beyond in detail were obtained. It is believed, however, that the generalizations are approximately true for the whole area of distribution.<sup>4</sup>

The grand period of growth falls in the warm season, when superficial soil-water is normally most abundant and when the night as well as the day temperatures are most effective. If the rainfall is subnormal, the drought so caused at this time results in very slow growth, made possible only by the meager amount of water that reaches the plant from the subsoil, derived in part from the earlier and usually small rainfall of the previous winter, together with the more immediately available supply from insufficient rains. This is only another way of saying that, in the region above described, water, as compared with the otherwise usually favorable conditions, is the prime condition for growth, and we may best see what the habits of the plant are by observing what growth takes place in relation to the rainfall. The extreme possibilities would be expected to be shown by plants under irrigation during every season. The observed growth in such plants, even in the presence of abundance of soil-moisture during November, December, and January, is exceedingly small in amount. Had the soil-moisture been reduced, say in September, so as to bring on a period of dormancy in the plant during October and November, it may well be believed that a much more marked growth might have occurred during the period following, when in point of fact little growth actually occurred. This behavior would be in accord with our general knowledge of growth-rhythm.

Although I have made no observation of positive value in this regard, it is said by supposedly competent observers that the guayule in the field may be expected to flower at any time, and that it has been seen to do so in every month of the year. Flowering, however, usually involves some foliage-stem growth as well; and so the evidence favors, or at any rate does not contradict, the view that growth may ensue at any time of the year. Because of the unfavorable night air-tempera-

<sup>1</sup> Cf. Livingston, 1906.

<sup>2</sup> Tolman, see Spalding, 1909.

<sup>3</sup> Escobar, 1910.

<sup>4</sup> Cf. Bray, 1906.

tures of the cooler period, however, the total amount of growth will not be great, to which result the less effective growing day temperatures contribute. The evidence shows further that growth in January, *e.g.*, will ensue upon a period of rest coupled with an unusually favorable rainfall, spread over time enough to produce a marked rise in the available soil-moisture as far down as the shallow roots. The times at which this conjunction of conditions may occur is indicated, negatively at least, when it is said that no growth in field plants was observed till May in spite of the rain, as indicated in table 1 and the accompanying diagram (fig. 3).

Not only, indeed, did no growth occur, but the guayule plants in the field in widely separated localities showed a marked need of water, a condition still more evident in April 1909. On the 11th of November, at Jaguey, 10 miles northeast from Cedros, the leaves were in a very much shriveled condition. Leaf-fall began toward the middle of December, the upper leaves, which are not cast off, being at this time in a distinctly flaccid condition. At this time the irrigated plants showed signs of leaf-fall, but for some time only the lowermost on the season's growth of stem were involved, while in the field plants all the fully developed leaves fell away at the same time.

Although, as above, seen it appears probable that growth may take place under favorable moisture conditions even in the winter, there is little evidence (Chapter III) that the amount is ever anything but small. The internodes are short, and thus is produced a crowding of the leaves, which by summer growth would be spread apart, and the structural marks between the two grand periods of growth are less obvious. As will be seen later, the dependence which may be placed in these marks as indicating the age of the plant is not materially disturbed by this circumstance:

#### RELATIVE HUMIDITY.

Unfortunately no instruments were available at Cedros for the study of relative humidity, and it is especially regretted that an atmometer after Livingston's design was not at hand. The only data obtainable, aside from my general observations, are those issued from the Observatorio de la Bufa at Zacatecas. A curve of tentative value based on these is presented in fig. 3, and, while this can be regarded as only approximate, it serves to indicate that the relative humidity is relatively high at Cedros (though not as high as at Zacatecas), and that there is a somewhat prolonged summer period of high humidity. The following remarks accord in general with these conclusions.

Dew is frequent during the cooler months, and was sufficient to run off the roof of the house occupied as a laboratory, the material being of painted canvas. The dew-point is always approached closely at night and usually passed in winter and during the rainy summer season. The high relative humidities which occur at all times during the night, and in certain situations during the day, at least during growing periods, are reflected in the vegetation. Only when this factor is taken into consideration can we explain the pronounced contrast seen between

the vegetations of the north and south facing slopes (Lloyd, 1909), and the peculiar distribution of certain plants, notably epiphytic species. A most instructive example is offered by *Tillandsia ciliata*, which is to be found epiphytic chiefly on the ocotillo (*Fouquieria splendens*), on slopes, mostly steep, where the drainage of cool air of high relative humidity passes downward from higher levels. The ocotillo itself grows in the more arid soil of southerly slopes. The *Tillandsia* ("pastle") occurs on other shrubs also wherever the most favorable humidity conditions are to be found, namely, in arroyos and narrow cañadas receiving air-drainage from adjacent high land, and I have seen a small amount in open flats many miles from the mountains, where, during the rainy season, water stands for some time over large areas,<sup>1</sup> thus producing similar conditions in less marked degree.

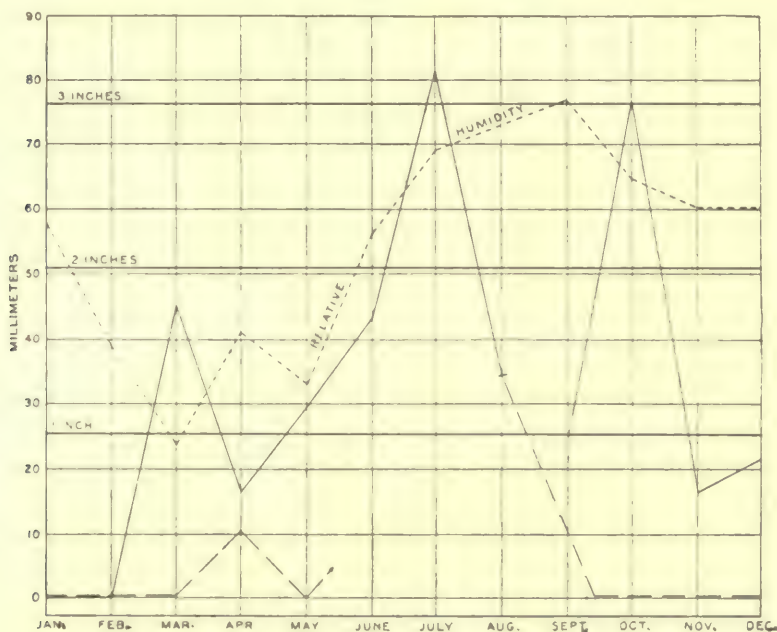


FIG. 3.—Monthly precipitation at Cedros, and relative humidity at Zacatecas city.

We may therefore conclude that the atmospheric humidity in this region is for a desert markedly favorable for vegetation, and may be called into account to explain the denser total growth of this desert as compared with the region immediately about Tucson, Arizona. What biological relations between plant structure and the conditions described above may be found is a problem for the future, the importance of which I have elsewhere pointed out (Lloyd, 1908b). Ross (1908) refers to the occurrence of dews in the guayule region and suggests that the dense trichome structure may be related to the absorption of atmospheric moisture, but offers no evidence. At the present time we may do little more

<sup>1</sup> As in the "laguna" in the Camacho bolson, east from that place.



than attribute to the high vapor-tension a general dampering effect upon evaporation, both from the plant and from the soil, but it is not improbable that research will discover plant-structures which are specifically related to atmospheric humidity, especially as it has been shown (Lloyd, 1905a) that the ocotillo and probably other plants have the ability to take advantage of rain which has not yet reached the earth.

### TOPOGRAPHY AND SOIL.

The surface of the high plateau of Mexico on which the guayule finds its home is broken up into mountain ranges of various extent, separated by wide, flat valleys or "*bolsones*." The middle reaches (playas) of these valleys are nearly level and have a deep, fine, alluvial soil, containing a vast amount of capillary water. In this soil the mesquite is generally found in abundance, and often of large size. Within these flats are frequently found more or less extensive areas (alkali spots, salt spots) where salts have accumulated and where the salt-bushes (*Atriplex* sp.) only may be found.

From the periphery of these alluvial plains, extending to the foot-hills of the mountain ridges, is a gentle slope of low gradient, the foot-slope, characterized by a gravelly soil (plate 5), which becomes more and more stony as the foot-hills are approached. Here the soil is frequently very shallow and may be confined to the crevices of the underlying rock. This condition becomes still more marked in the hills proper, where the edges of the strata are often exposed and where the vegetation is confined to the intervening fissures. The most widely distributed plants of the foot-slope and adjacent ridges, and therefore the most characteristic, are the alvarda or ocotillo (*Fouquieria splendens*), the palma samandoca (*Samuella carnerosa* Trelease), and the Cedros sotol (*Dasyllirion cedrosanum* Trelease).<sup>1</sup> The gobernadora or Mexican greasewood (*Covillea* sp.) is also a very common plant of the foot-slopes and ridges, but is to be found also in the alluvial plains and is therefore less characteristic.

Of the species of *Parthenium* found in the region, the guayule is confined to the foot-slopes and foot-hills,<sup>2</sup> being also abundant in hills not above about 7,000 feet in altitude. It is therefore, like some of its

<sup>1</sup> *Dasyllirion cedrosanum* Trelease (n. sp.).

Subacaulescent. Leaves slightly roughened on the dorsal angles, pale, the upper face glaucous, somewhat fibrous-brushy at tip, broad (20 mm.), 1.5 m. or more long: prickles mostly 10 to 15 mm. apart, yellow or at length reddened at tip, 3 to 5 mm. long, moderately heavy, upcurved or hooked, the whitish-yellow intervening margin roughened by minute hyaline tipped denticles. Branches of the narrow inflorescence rather elongated, about 7 by 60 mm. Fruit narrowly elliptical, 4 to 5 by 7 to 9 mm., deeply and acutely notched, the style much shorter than the wings.

Cedros, Zac., Mexico, Lloyd, No. 118—the type, No. 82, 1908; Kirkwood, No. 96, 1908.

Allied to *D. wheeleri* and *D. graminifolium*, from both of which it differs in its smaller fruit not widened upwardly and with shorter style more conspicuously surpassed by the wings (fig. 4, and on the extreme right of fig. A., pl. 1).

The type is in the Herbarium of the Missouri Botanical Garden; cotypes in the Gray and National herbaria.

<sup>2</sup> It is generally believed by those familiar with the plant that it affects more particularly the south slopes, and this accords in general with my observations, though it must not be inferred that it does not grow at all on north slopes.

associates above mentioned, an "edaphic" species, found only where the ground is stony. In the alluvial plains one meets only an occasional isolated plant, but if the plain is traversed by a low ridge of gravelly ground, even if the surface is raised only a few inches above the surrounding area, the guayule may be found. In the fine soil of the plain, on the other hand, the mariola (*Prathenium incanum* H. B. K.) and the annual species *P. hysterochorus* grow in abundance, though the mariola is commonly associated with guayule on the foot-slopes and hills. This association of guayule and mariola frequently misleads the inexperienced observer in estimating the amount of guayule which may be found in a given area.

Why the guayule does not grow in the fine alluvium is not clear, and is a question often asked by persons familiar with the facts. Any reasons, aside from those mentioned above, which may be assigned are at present of only speculative value, but some reference may properly be made to them.



FIG. 4. *Desertion cedrosanum* Trelease. Type material in the lower row. Above, for comparison fruits of *D. wheeleri* at the left and of *D. graminifolium* at the right.  $\times 3/1$ .

Guayule is confined practically to the Cretaceous region of the Central Plateau, and therefore to highly calcareous soil (see Chapter IX). It may very well be that the plant is sensitive to even a slight acidity, and therefore prefers a soil with a very small amount of humus. Certain experimental results referred to beyond, while not conclusive, indicate that this explanation may apply during the period of germination, but it has been found that the absence of lime is not a hindrance to maturer plants.

It is a popular notion that the plant "rots" in situations where water is relatively abundant, and that for this reason it is not to be found in "bajillos" or low places. It is true that for a considerable period in the summer season practically mesophytic conditions prevail in many areas within the flats, especially in the frequent slight depressions. Here annual weeds grow in profusion, and a number of species of desert shrubs flourish. Among these is the mariola, the seeds of which germinate freely among the dense vegetation of shrub and weed, and in one season





A



B

A. Station 2, Quadrats 5 and 6, foot-slope of Sierra Zuluaga.

B. Station 3, Quadrat 1, near Cedros. A good stand of mature plants.







Plants from Quadrats 5 and 6, Station 2.





attain a height of a foot or two; but this is not true of the guayule. That, however, the mere quantity of water or the density of the vegetation are not the determining factors is shown by experimental evidence, while in the field are to be found numerous instances of plants which have germinated in the dense shade and dampness found beneath the dead leaves of the sotol and in crowded conditions produced by other plants, such as the lechuguilla. Indeed, these are frequently the only conditions under which the plant gains a foothold. It therefore does not appear probable that the abundance of water or the density of the vegetation is the determining factor in preventing the guayule from getting a start; hence we may infer that the conditions below the surface must be understood before an explanation may be had. The edaphic habitat of the plant suggests that the mechanical conditions of the alluvial soil are unfavorable, owing to meager aeration, in connection with which the humus conditions also may have to be taken into account.

#### DENSITY OF GROWTH.

Of great importance economically as well as to the student of vegetational problems is the number of plants per unit of area, both absolute and relative. The operations of the forester rest upon this datum in the first instance, as this, together with the size of the individuals, forms the basis of calculations of the available tonnage per acre. It will readily be understood that any estimate on a large scale will involve a necessarily large error, since it would be impossible to do more than proceed on the basis of sample counts combined with acreage and estimates of size. This can frequently be done with great accuracy by persons who have had practical experience in taking guayule from the field, especially if the judgment be checked by survey and sample counting and weighing. The following tables, the data for which were obtained by accurate measurement, will, however, serve a useful purpose in indicating a method of making estimates, as well as in furnishing indications of actual conditions. For the purpose, quadrats of 100 square meters were laid out by means of a steel tape, the data obtained attaching to the guayule plants within each such quadrat.

The weights in the following tables are field weights. For dry weights a reduction of 20 to 25 per cent is necessary. As field weight is usually assumed, however, I have followed the usage and have not applied the above correction.

TABLE 4.

Two adjoining quadrats, each of 100 sq. meters, on a loma or ridge extending toward the Sierra Zuluago, about 10 miles north of Cedros (plate 5, fig. A). All the plants were pulled up and sorted, each package containing plants of similar size and habit. The packages were then grouped into classes arbitrarily, and a typical plant for each class photographed (plate 6). The age of this plant was carefully estimated and checked by estimating the ages of a number of similar plants. (March 29, 1908.)

Class.	No. of plants in package.	Weight of package.	Average weight of individuals.	Estimated age.	Average height of class.
		<i>lbs.</i>	<i>lbs.</i>	<i>years.</i>	<i>cm.</i>
I.....	{ 20 20 20 20	{ 15 17 22.5 17	{ 0.75 0.85 1.12 0.85	15 to 18	58
II.....	{ 20 20 20 20 20 20	{ 13 10.5 9 10.5 9.5 12	{ 0.65 0.52 0.45 0.52 0.47 0.6	11 to 13	30
III.....	{ 50 40 40 40	{ 19 10.25 11.5 10	{ 0.38 0.25 0.29 0.25	7 to 10	25
IV.....	{ 60 120 50 70	{ 8.25 18 7.5 11	{ 0.14 0.15 0.14 0.16	5 to 7	20
V.....	{ 60 80 60 100 183 100 100 18	{ 7 8 6 7.75 18.25 12.5 10 2	{ 0.11 0.1 0.1 0.08 0.1 0.12 0.1 0.11	1 to 5	15
Total <sup>1</sup> .....	1371	303.0	.....	.....	...

<sup>1</sup> 685 plants in 100 square meters.

Class V is made up of all sizes up to the maximum indicated. In plate 6, figs. 5 to 7, examples of three sizes and ages are shown. The weights and estimated ages of all the plants in plate 6 are shown in table 5.

TABLE 5.

Class.	Age.	Height.	Weight.
	<i>years.</i>	<i>cm.</i>	<i>oz.</i>
I.....	15	58	18.5
II.....	11	30	6.
III.....	8	25	1.875
IV.....	7	20	0.875
V.....	5	15	0.5
VI.....	2	..	0.05
VII.....	1	..	.....

TABLE 6.—Station 8, quadrat 2 (100 square meters on low ridge just north of Cedros).

Class.	No. of plants in class.	Total weight.	Individual weight.	Height.	Age.
		<i>lbs. oz.</i>	<i>lbs. oz.</i>	<i>cm.</i>	<i>years.</i>
I.....	I	3 14	3 14	70	(1)
	I	3 10	3 10	60	20
	I	3 10	3 10	70	22
	I	3 6	3 6	60	15 to 18
	3	10 8	3 8	60 to 68	20
II.....	4	9 14	2 7.5	45 to 55	16 to 18
	I	2 4	2 4	68	20 (about)
	I	2 4	2 4	55	20
	I	2 8	2 8	50	15 to 18
	I	2 10	2 10	50	15 to 18
	I	2 10	2 10	70	(1)
III.....	4	8 14	2 3.5	45 to 50	<sup>2</sup> 18 to 20
	4	6 8	I 10	40 to 45	15
	I	I 4	I 4	46	15
	I	I 14	I 14	65	17 to 18
	4	6 14	I 11.5	45 to 50	15
	I	I 00	I 00	40	7 or 8
	I	I 3	I 3	37	7 or 9
	I	I 6	I 6	40	10 to 12
IV.....	I	I 7	I 7	43	12
	I	I 00	I 00	35	9
	2	I 14	.. 15	40	7 to 8
	2	I 14	.. 15	35	<sup>2</sup> 10 to 15
	I	I 11	.. 11	35	10
	I	I 11	.. 11	40	8
V.....	2	I 6	.. 11	38	<sup>3</sup> 15
	2	I 4	.. 10	40	..
	I	.. 8	.. 8	35	<sup>2</sup> 9 to 10
	I	.. 6	.. 6	30	9
	I	.. 4	.. 4	30	8
	I	.. 3	.. 3	30	10
	I	.. 2.75	.. 2.375	27	6 to 7
	I	.. 2.125	.. 2.125	23	5
	I	.. 2.125	.. 2.125	27	6 to 7
	I	.. 1.5	.. 1.5	20	(2)
	2	.. 3.75	.. 1.875	27	6 to 7
	I	.. 1.125	.. 1.125	20	5
	2	.. .875	.. 1.5	13	3 to 4
	14	( <sup>5</sup> )	.. ..	....	I
	3 <sup>4</sup>	( <sup>5</sup> )	.. ..	....	....
Total.....	75	<sup>6</sup> 83 14	.. ..	....	....

<sup>1</sup> Old scraggly plants whose age it was impossible to determine even approximately.<sup>2</sup> Slowly growing, densely branched plants.<sup>3</sup> Tall and slender.<sup>4</sup> Retoños.<sup>5</sup> Very small.<sup>6</sup> Classes I-IV, inclusive.



TABLE 7.—Station 8, quadrat 1 (100 square meters on low ridge just north of Cedros, July 20, 1908).

Class.	No. of plants in package.	Total weight.		Individual weight.		Height.
		lbs.	oz.	lbs.	oz.	cm.
I.....	1	6	4	6	4	70
	1	6	4	6	4	..
	1	4	8	4	8	..
	1	4	2	4	2	60 to 70
	1	4	6	4	6	..
	1	4	3	4	6	..
	1	4	2	4	2	60 to 70
II.....	1	3	14	3	14	..
	1	3	10	3	10	60
	1	3	10	3	10	..
	1	3	4	3	4	40 to 45
	1	3	00	3	00	50 to 60
III....	1	2	14	2	14	..
	1	2	12	2	12	55
	1	2	12	2	12	..
	1	2	12	2	12	..
	1	2	8	2	8	..
	2	4	8	2	4	..
	1	2	00	2	00	..
	1	10	00	2	00	..
	5	10	00	2	00	..
IV...	1	1	00	1	00	..
	10	10	2	1	0.2	..
	10	10	12	1	1	..
	10	11	12	1	3	45
	1	1	6	1	6	45
	1	1	10	1	10	..
	1	1	12	1	12	..
	6	10	12	1	13	45 to 60
V...	4	3	00	..	12	35
	2 <sup>1</sup>	..	8	..	..	30 to 35
	5	1	00	..	3	30
	5	..	4	..	0.8	15 to 20
Total	81	135	5	..	..	.....

<sup>1</sup> Retones.

TABLE 8.—Station 9, quadrat I (100 square meters, on a 25-degree northeast slope, in the hills east of Cedros).

Class.	No. of plants in package.	Total weight.		Individual weight.		Height.
		lbs.	oz.	lbs.	oz.	
I.....	{ I	3	12	3	12	60 to 65
	{ I	3	8	3	8	60
II.....	{ 2	4	10	2	5	50 to 60
	{ 2	4	4	2	2	55
	{ 2	4	6	2	3	35 to 40
	{ 5	11	0	2	3	60
	{ I	2	0	2	0	45
III.....	{ 5	9	6	I	14	40 to 45
	{ 3	5	8	I	13	50
	{ I	I	10	I	10	50
	{ 2	3	0	I	8	60
	{ 5	6	12	I	5.6	40
	{ I	I	4	I	4	45
	{ 2	2	4	I	2	45
	{ I	I	0	I	0	40
IV.....	{ 4	3	12	..	15	35
	{ I	..	10	..	10	45
	{ 4	2	2	..	8.5	25 to 35
	{ I	..	..	..	5	..
	{ I	..	..	..	3.5	..
	{ I	..	..	..	2.125	..
	{ 2	..	3.25	..	1.625	..
	{ I	..	..	..	1.5	..
	{ I	..	..	..	1.375	..
	{ I	..	..	..	1.25	..
	{ I	..	..	..	1.18	..
	{ I	..	..	..	.875	..
	{ I	..	..	..	.75	..
	{ 2	..	1.25	..	.625	..
	{ I	..	..	..	.5	..
	{ 20	..	5	..	.25	..
	{ 20	..	1.375	..	.06	..
	{ 20	..	1.31	..	..	..
	{ 4	..	.125	..	.03	..
	{ 8	..	.125	..	.015	..
	{ 14	..	..	..	..	..
Total.....	133	<sup>2</sup> 63	..	..	..	..

<sup>1</sup> Retoños of small size.<sup>2</sup> Total weight, classes I to III, inclusive.

TABLE 9.—Station 2, quadrat 7, April 3, 1909.

[The data for this table were obtained by pulling up, sorting, and weighing all the plants on 100 square meters in a guayule field from which all the plants above 40 cm. tall had already been taken. (Plate 1, fig. A.)]

No. of plants.	Weight.		Average weight.	Height.
	lbs.	oz.	oz.	cm.
100	25	8	4	25 to 35
60	11	..	3	30
60	12	..	3.2	25 to 53
60	10	8	2.8	20 to 35
31	7	4	3.7	25 to 30
60	13	..	3.5	22 to 30
50	4	8	1.4	20 to 30
50	7	4	2.32	20 to 25
50	6	12	2	20 to 25
50	4	4	1.26	20 to 25
50	5	8	1.76	20 to 25
64	3	4	0.8	18 to 20
61	2	..	0.5	15
10	..	0.125	....	.....
755	112	12.125	....	.....

<sup>1</sup> All seedlings of 1908, except one of 1907.

TABLE 10.—Station 9, quadrat 2, April 14, 1909 (100 square meters, ridge of loma in hills (El Potrero), east of Cedros).

No. of plants.	Weight.		Average weight.	Height.	Remarks.
	lbs.	oz.	oz.	cm.	
1	4	4	68	70	Scrubby.
1	3	..	48	65	
1	3	..	48	65	
1	2	8	40	63	
1	3	12	60	62	
1	1	12	28	60	Rather scrubby. Do.
1	2	4	36	60	
1	2	..	32	57	
1	1	12	28	55	Spread 100 cm.
1	2	..	36	53	
1	5	12	92	50	
1	2	4	36	50	4 to 5 years seedling. Badly developed. Seedling, 5 years. 3 years retoño. Seedling, 2 years. Seedling, 3 years.
2	2	12	22	44	
4	3	12	15	40	
1	..	3.5	3.5	24	
1	..	1	1	24	
1	..	2.5	2.5	23	
1	..	2.5	2.5	16	
1	..	0.5	0.5	11	
1	..	0.5	0.5	14	
24	41	6	....	...	



TABLE 11.—Station 10, April 5, 1909 (quadrat of 100 square meters).  
[On a southerly slope 10 kilometers north of the Cerritos de los Calzones.]

No. of plants.	Weight.		Average weight.	Height.	Remarks.
	lbs.	oz.	oz.	cm.	
1	2	4	36	65	NOTE.—The shrub of this region is rough looking and rather badly attacked by insects. A good deal of witches' broom, and many plants attacked at the base by borers.
1	..	8	8	50	
3	4	4	23	40 to 50	
5	6	..	19	40 to 50	
5	9	..	29	45	
6	6	12	18	35 to 50	
4	5	8	22	30 to 50	
8	6	4	12.5	35 to 40	
8	6	..	12	35 to 40	
2	..	8	4	30 to 40	
7	6	8	14.8	30 to 40	
5	5	12	18	35	
7	5	8	12.6	35	
10	6	..	9.6	35	
8	6	8	13	35	
5	3	8	11.2	30 to 35	
16	4	..	4	30 to 35	
5	4	..	13	25 to 35	
10	3	..	4.8	20 to 40	
10	2	8	4.4	25 to 30	
16	2	12	2.75	25	
12	14	..	5.3	20 to 30	Seedlings, 2 to 3 years old. Seedlings, 2 years old. Seedlings, about 3 yrs. old Retoños. Small plants.
6	..	4	0.6	15 to 20	
7	..	..	....	.....	
1	..	..	....	.....	
7	..	..	....	.....	
8	..	..	....	.....	
3	..	..	....	.....	
186	101	4	....	.....	

<sup>1</sup> Scant.

TABLE 12.—Station 11, near Caopas, April 6, 1909.

No. of plants.	Weight.		Average weight.	Height.
	lbs.	oz.	oz.	cm.
1	2	6	38	50
1	1	10	26	50
5	5	8	17.6	40 to 50
5	7	4	22	35 to 40
6	6	0	16	35 to 40
1	1	....	16	35
8	6	....	12	30 to 40
5	5	....	16	30 to 40
7	5	....	11.4	30 to 40
8	4	....	8	30 to 35
9	2	8	4.4	30 to 35
8	2	8	5	30
12	4	12	6.3	30
15	2	....	2.1	25
21	3	....	2.3	20 to 30
12	2	8	3.3	20 to 25
37	3	8	1.5	20 to 25
10	2	8	4	20 to 25
25	2	4	1.4	20
30	1	....	0.5	20
17	..	10	0.6	15 to 20
21	..	4	0.2	15
3	..	2.5	0.8	15
12	..	10	0.8	10 to 15
279	171	14.5	....	.....

<sup>1</sup> 7,100 pounds per hectare.

TABLE 13.—Station 12, foot-slope ridges south from Apizolaya, April 10, 1909. (Plate 7, and plate 1, fig. B.)

No. of plants.	Weight.		Average weight.	Height.
	lbs.	oz.	oz.	cm.
2	4	8	35	60 to 70
5	10	.....	32	60 to 70
5	10	.....	32	60 to 70
5	9	8	30.4	60 to 70
5	9	8	30.4	60 to 70
5	9	.....	28.8	60 to 70
5	9	.....	28.8	60 to 70
5	8	.....	25.6	60 to 70
5	7	12	24.8	60 to 70
5	7	.....	22.4	60 to 70
5	6	8	20.8	60 to 70
1	3	.....	48	60
5	9	8	30.4	60
0	6	.....	10.7	60
5	2	8	8	50
7	3	.....	7	50
0	4	.....	7.1	50
7	3	8	8	50
5	4	4	13.6	40 to 50
6	4	8	12	45
5	4	.....	12.8	40
5	3	8	11.2	40
5	4	4	13.6	40 (1 at 50)
10	3	.....	4.8	40
6	5	4	14	35 to 45
10	2	4	3.6	35 to 40
12	2	4	3	30
25	2	.....	1.3	30
20	3	4	2.6	30
25	2	8	1.6	30
28	1	12	1	25 to 30
20	2	12	2.2	25 to 30
..	..	10	5	30
13	..	6.5	.....	18 to 23
4	..	2.75	.....	18 to 23
5	..	3.5	.....	22
Add, making additional weight—				
10	3	4	.....	40 to 60 (scrappy)
Scraps...	4	.....	.....	
311	172	5	.....	

Summarizing the above results, and including data from other sources, we have as follows:

Station.	Quadrat.	No. of plants.	Station.	Quadrat.	No. of plants.
4	1	50	8	1	81
5	1	275	9	1	130
2	3	360	7	7	755
2	4	270	9	2	24
2	1	285	10	..	186
3	1	30	11	..	279
2	15 and 6	685	12	..	311
8	2	75			

<sup>1</sup> Averaged.



A



B

A. Quadrats (station 12) in a very dense growth. Apizolaya.  
B. The same, the guayule removed.





Here there is a range in numbers of plants from 2,400 to 75,500 plants per hectare, but the meaning of these figures can not be understood unless the size of the plants is taken into consideration. From the point of view of business opportunism, a stand of 2,400 plants per hectare may be better than one of much higher figures, while for one who is looking for a basis for permanent investment other questions of relative sizes and numbers of plants arise, the answer to which involves an explanation of the rate of reproduction in the field. This subject will be treated in detail in Chapter IV, it being our purpose here to show the actual condition as viewed by one who is estimating the tonnage per unit of area.

If we refer back to table 4, we will observe that the two quadrats contained 1,371 plants, the average weight of which was a little over 3.5 ounces. Of these, however, only 80 were large enough to be gathered, namely, those about 1 pound or over in weight; though if the land were being exploited smaller ones would be taken, say those weighing above half a pound. This would include all of the plants in classes 1 and 11, weighing in the aggregate about 58.75 pounds, or 5,875 pounds per hectare, assuming the quadrats to be fair samples, or about 2.67 tons (long).

Treating the remaining tables similarly, we have the following figures:

TABLE 14.

Table No.	No. plants above 8 ounces.	Weight of these.		Weight per hectare.		No. plants below 8 ounces.	Average weight of available plants.	
		lbs.	oz.	lbs.	tons (long).		lbs.	oz.
4	80	58	12	5,375	2.4 +	605	0	11.75
6	45	83	14	8,390	3.7	30	1	13.8
7	69	131	7	13,140	6 —	12	1	14.5
8	43	69	8	6,950	3.1	90	1	9.8
10	18	40	5	4,033	1.8	6	2	5.8
11	114	83	8	8,350	3.7	98	0	11.7
12	47	43	12	4,374	2 —	232		14.9
13	113	137	0	13,700	6.1	200	1	3.4

It will need but a glance at the above summary to show that, from the business point of view, the acreage of large but comparatively few plants is the more valuable to the purchaser who is not looking to the future, for the reason that the cost of harvesting a small number of large plants will be less than if the available plants are large in number and of smaller size, and because the larger plants can be handled more readily and therefore more cheaply. Furthermore, it is much easier to determine the tonnage with fair accuracy where the plants are few and large. The error due to applying data taken from small sample areas to an extensive area within which the sample area falls, must of necessity be large, for the number of plants as well as their character must be considered. Taking the question of number alone, the size of the error on this score will be appreciated when it is known that on an area of 42.7 acres at Station 2 (plate 1) 181 bales of guayule, or at the

rate of about 800 pounds per acre (1,976 pounds per hectare), were actually collected. As this was gathered under the rule that no plants less than 40 cm. in height or in spread were to be taken, some plants which would run over 8 ounces were doubtless left, but allowing for this error probably not more than 2,000 pounds to the hectare could have been taken, or at most 1 ton of 2,200 pounds. On another area of 30.8 acres of the same general character, but of thinner stand, 53 bales or at the rate of 344 pounds per acre (about 850 pounds per hectare) were gathered.

It will thus be seen that the difficulty in estimating tonnage per unit of area with small error is at best very great, and this, as already said, is rendered more so by the difference in the character of the plants. To judge of the truth of this, one has but to examine the various illustrations accompanying this paper. In particular, a comparison of two prevalent types is shown in plate 8, namely, a slender and a spreading type, but neither of extreme form.

TABLE 15.—*Dimensions of narrow and spreading types of shrub, illustrated in plate 8.*

Narrow type.					Spreading type.						
Plant.	Weight fresh.		Weight dry.		Height.	Plant.	Weight fresh.		Weight dry.		Height.
	lbs.	oz.	lbs.	oz.	cm.		lbs.	oz.	lbs.	oz.	cm.
A	4	0	2	11	65	A	3	6	2	4	50
B	2	0	1	2	48	B	2	12	1	13	45
C	1	2	..	15	46	C	1	0	..	14	33
D	..	8	..	5.5	33	D	..	6	..	5	23
E	..	6	..	4	28	E	..	5	..	3.75	21
F	..	3	..	1.5	24	F	..	1.75	..	0.93	17
G	..	1.25	..	0.5	23						

From the above data it is seen that, speaking broadly, the weight of plants of the spreading habit is one-third to one-half greater than those of the narrow type of similar height, so that a stand of the latter must have a density correspondingly greater to equal in total weight a given stand of the spreading type.

As one looks over a "field" of guayule, these apparently minor differences of form are not at all apparent, because of the interference of other vegetation with the vision. If the occasion presents itself when more accurate estimates will be demanded than at present, this condition will have to be taken into account. It should be further mentioned that the weights given above are of freshly gathered plants. If it is desired to calculate to "air-dry" shrub, the proper correction should be applied, but as this is very variable, according to the season, no constant can be given. It may, however, be as great as 22 per cent in the dry season.

The only other published calculations of this kind were made by Endlich (1905, p. 1118), who, for the purpose of calculating the area of guayule land necessary to support the industry, assumes the average weight of the plant to be 500 grams, and the density of growth to be, by weight, 500 to 800 kilograms per hectare, or from 1,000 to 1,600



plants per hectare of 500 grams average weight, taking into account the unevenness of distribution, that is, the more or less extended areas where guayule does not occur. The following figures are deduced from the quadrats above detailed, taking *all* the plants into account :

TABLE 16.—*Number of plants in given areas.*

Table Nos. recording quadrats.	No. of plants per hectare.	Average weight.		Kilograms per hectare.
		Ounces.	Grams.	
4	68,500	3.5	99.2	6,795.2
6	7,500	18.4	521.6	3,912
7	8,100	26.56	753.0	6,099
8	13,300	8.5	241.0	3,205
10	2,400	27.2	771.1	1,850.64
11	18,600	8.71	246.9	4,592.34
12	27,900	4.12	116.79	3,258.72
13	31,100	8.86	252.97	7,867.36
Ave..	22,175	13.2	375.3	4,672.53

From the above it is seen that the average in long tons per hectare is 4.67, per acre 1.85.

The average weight of all the plants on the quadrats is thus seen to be less than Endlich's estimate by 125 grams, or one-fourth, and as these sample areas include the very best guayule land, that is, the densest areas with the largest plants in relation to the density, it may be concluded that the present estimate is more nearly correct. In estimating the average density over large areas, great difficulties are met. Endlich assumed one-tenth of the area of the guayule region to be occupied by the shrub at an average density of 500 to 800 kilograms per hectare. This figure does not approach the indications of our data, though it must be remembered that these do not take into account poor areas where the shrub is very scattering or nearly absent—as the Mexican well expresses it "salteadito." For certain areas, *e.g.*, one of 1,800,000 acres (728,744 hectares) which has been somewhat closely studied for the special purpose of estimating the amount of shrub to be found there, Endlich's factor was found to be very small, for if only one-hundredth of its area carried guayule in the quantity of our general average, there would be as much as of one-tenth of it which carried shrub of the amount of his factor. We may feel sure, however, that our average applies to more than one-hundredth of the total area. Whether Endlich's figure applies better to the total guayule area of Mexico can not be said with any certainty, but it is only fair to say that, in view of the great difficulties involved, it is probably as near the truth as any that we might venture.

## BIOTIC RELATIONS.

## COMPETITION.

The relation of guayule to the other plants with which it is commonly found associated is of great importance, especially if forestry methods are contemplated. Both the mutual effect of each element in the vegetation upon the guayule and the relative rate of growth must be understood in order to judge what the final effect in the struggle for existence is likely to be. To do this, however, involves a very considerable amount of sustained observation by means of the quadrat method, first devised by Clements. Following is a census of the more important plants found growing in association with the guayule in quadrats 5 and 6, Station 2.

TABLE 17.

Scientific name.	Common name.	Total No. in 200 square meters.
<i>Parthenium argentatum</i> .....	Guayule.....	1371
<i>Agave lecheguilla</i> .....	Lechuguilla.....	50
<i>Covillea mexicana</i> .....	Gobernadora.....	6
<i>Samuella carnerosa</i> .....	Palma samandoca.....	4
<i>Dasyliion cedrosanum</i> .....	Sotol.....	1
<i>Acacia farnesiana</i> .....	Huisache.....	7
<i>Jatropha spatulata</i> .....	Sangre de drago.....	Scattered all over.
<i>Zexmenia brevifolia</i> .....		6
<i>Lophophora williamsii</i> .....	Peyote (peyotl).....	about 20
<i>Opuntia megalarthra</i> .....	Rastrero.....	45

Also the following, from Station 10:

TABLE 18.

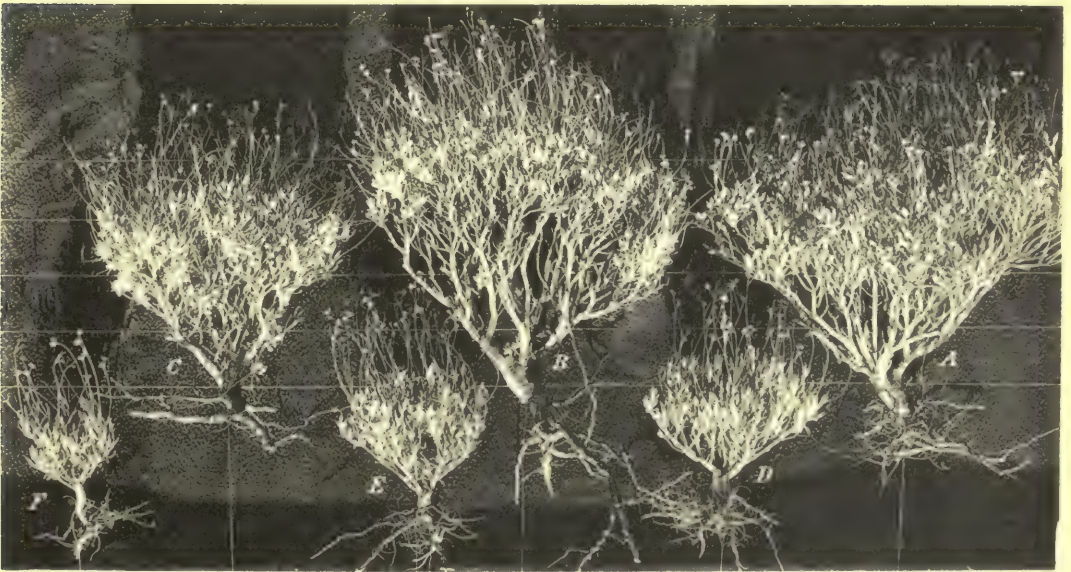
Scientific name.	Common name.	No. in 100 square meters.
<i>Parthenium argentatum</i> .....	Guayule.....	186
<i>Parthenium incanum</i> .....	Mariola.....	14
<i>Opuntia stenopetala</i> .....	Nopal colorado.....	5
<i>Opuntia microdasys</i> .....	Segador.....	7
<i>Covillea mexicana</i> .....	Gobernadora.....	8
<i>Opuntia imbricata</i> .....	Gardenche.....	1
<i>Salvia chamædryoides</i> .....	Engorda cabra.....	3
<i>Dasyliion cedrosanum</i> .....	Sotol.....	1
	Cacti.....	Several small inconspicuous plants.
<i>Samuella carnerosa</i> .....	Palma samandoca.	
<i>Agave asperrima</i> .....	Maguey.	

With few exceptions, these constitute the dominant vegetation of the foot-slopes and the low ridges, though of course a number of other species may be found in other localities, and indeed may be more important elements elsewhere than has been observed to be the case in North Zacatecas.





A



B

A. Narrow type of guayule. B. Spreading type of guayule. (See table 15.)





A few of the more obvious of these are:

Scientific name.	Common name.
Echinocactus palmeri.....	Biznaga burra.
Fouquieria splendens.....	Ocotillo or alvarda.
Echinocactus pringlei.....	Biznaga colorada.
Buddleia marrubifolia.....	Asafran.

The above enumeration indicates that at the present time the guayule in this habitat is far and away the most important plant numerically, and is therefore dominant in the usual sense. Whether it will continue so—whether its dominance is waxing or waning—may be indicated by the relative numbers of guayule plants of different ages and by the interaction of the various elements in the vegetation.

We may therefore consider briefly each of the numerically most important species.

#### LECHUGUILLA (AGAVE LECHUGUILLA).

While the actual number of plants of this species found in quadrats 5 and 6 is much larger than that of any other save guayule, it is very small compared with the number which is found on much guayule land (*e.g.*, plate 5, fig. B).

In common with the *Agaveæ*, the plant propagates itself chiefly by means of stolons which lie a few centimeters below the surface. In this way it spreads from an original plant radially, taking up the ground as it goes, from which nothing but death dislodges it. In the course of a few years it attains maturity, when a tall flower-stalk is developed; then the whole individual, consisting of a single cluster of leaves attached to a short (10 to 15 cm.) and thick (6 to 7 cm.) stem, dies. Where the lechuguilla has occupied the ground for some time, it frequently forms a dense growth, from which other plants, save a few annuals or emaciated perennials, are excluded. Its manner of spreading, by which it reproduces itself vegetatively, enables the plant to occupy areas in which the soil is confined to the crevices of the rocks, and in this manner it may occupy ground which is unfit even for those desert plants with which it is usually associated. From it is extracted the fiber "ixtle tula," or "ixtle de lechuguilla," which is of considerable commercial importance, and thus the plant is of some value—not, however, sufficient to justify it as a competitor of the guayule. The method of vegetative reproduction above noted is also characteristic of the guayule (Lloyd, 1908*c*), especially when growing where the country rocks come to the surface, but is in this plant of relatively much less importance.

The mutual behavior of these two plants under strong competition is not very easy to describe precisely. It seems clear that, with the exception of a few plants which succeed in gaining a foothold by germinating in the shade between plants of lechuguilla, sometimes being favored by the protection from drying out and from cropping by animals thus afforded, ground occupied by lechuguilla is much less favorable for the

growth of guayule than that from which lechuguilla is absent. For although it would seem that germination and early growth are favored by the protection offered by the lechuguilla, as a matter of observation one finds but few young plants of guayule in such situations. One reason for this is, probably, that the guayule seeds (achenes) find difficulty in reaching the soil, because the leaves of the lechuguilla catch them and hold them in their axils till they die, thus materially reducing the numbers which reach the ground. Aside from the consideration that the lechuguilla takes up from the soil its quantum of water, its effect upon guayule is unfavorable, therefore, because of its superior powers of progressively and steadily occupying the ground, and because of the loss of guayule seed by being caught in its leaves. Lechuguilla appears to be an increasingly dominating type in every situation where it gains a foothold. It is common to every part of the foot-slope and in the hills throughout the range of guayule. The great quantity of it to be found produces in many parts of the mesa central the dominating yellow-green coloring often seen there. When it and the guayule are associated, the green is dotted by the gray of the latter, although other plants also may contribute this subdued note in the coloring.

GOBERNADORA (*COVILLEA TRIDENTATA*) AND OCOTILLO (*FOUQUIERIA SPLENDENS*).

These may be considered together. Their forms are similar because of the habit of their slender branches, which arise from near the base and reach obliquely upward, producing the effect of an inverted cone. They are both taller than guayule, but the shade cast by them is small in amount, and less is cast by the ocotillo than by the gobernadora. The only places where the ocotillo grows thickly are in certain situations on south slopes, and here it often forms a dense thicket. When thickly growing it would interfere with the rapid harvesting of guayule because of the thorny branches, but, excepting for the draft it makes on the soil for water, the effect upon guayule is negligible. This applies about equally to gobernadora, which in North Zacatecas, however, reproduces itself quite rapidly by seed, and so may readily come to occupy too much ground.

PALMA SAMANDOCA (*SAMUELLA CARNEROSA*) AND SOTOL (*DASYLIRION CEDROSANUM*).

These are similar in form. Each plant has a single stem supporting a large rosette of leaves. The sotol, however, rarely rises sufficiently above the surface of the soil to free the surface from the lower dead leaves, which cover about 10 square feet of area. Both plants are valuable economically, the palma samandoca affording a fiber of less value than the lechuguilla, but of which a good deal is prepared, while the other is the basis for the manufacture of the whisky-like liquor, mescal sotol, or simply sotol. Neither of these occurs in sufficient numbers to figure in competition with the guayule within its proper habitat. Indeed, for reasons not yet understood, when sotol grows densely, forming a chaparral, guayule is entirely absent. One reason, if not the only important one, is that the sotol appears not to be confined to limestone areas, but is not excluded from them.



SANGRE DE DRAGO (*JATROPHA SPATULATA*).

This plant is a very characteristic xerophyte, and is found beyond the limits of the Chihuahuan desert, westward into Sonora (MacDougal, 1908). The upper part of the plant consists of a simple, dark-brown and somewhat fleshy stem, scarcely branched at all and slightly curved. The leaf-producing lateral shoots are very short, and are roughened with small scales; from them arise the bright green narrow leaves in clusters. Reproduction takes place readily by means of seed, and the plant spreads by underground stems which are thick and fleshy, and are, in fact, water-storage organs. Like the lechuguilla it is a colonial form, growing in dense patches, but is less able to occupy the ground to the exclusion of other plants because of the slender aerial parts. Its ability to take up large amounts of water from the superficial soil must, however, be reckoned with. There is little doubt that this is a dominating type.

RASTRERO (*OPUNTIA MEGALARTHRA*).

This is a spreading, low form of prickly pear. Though sometimes very densely packed, making progress difficult, mechanically it interferes comparatively little with guayule. This is to be explained by the fact that, on account of the edgewise position of the flat, procumbent branches, very little soil surface is actually occupied. One finds, indeed, that young plants of guayule are frequently abundant in irregular rows beneath, or nearly so, the branches of the opuntia. It is not unlikely that the spines of the former aid somewhat in protecting the guayule from jack-rabbits and other predatory animals, and so, in this particular respect, help it along rather than hinder it. While this opuntia is a persistent type, its occupancy of the ground is apparent rather than real.

A composite shrub (*Zexmenia brevifolia*), huisache (*Acacia farnesiana*), gatuño (*Acacia greggii*), and safran (*Buddleia marrubiiifolia*) are all shrubby, freely branching kinds. The last resembles guayule in color, and the novice may easily mistake the one for the other. The gatuño and huisache are small trees with slender branches, and make but little shade. The nature of the competition between these forms and lechuguilla is more evident than in the case of these and guayule. They are slow-growing and do not reproduce themselves except by seed, and this not rapidly. Nevertheless, excepting the gatuño, they may be found growing very plentifully in some situations and often outnumber the guayule. Thus on north slopes the composite shrub is frequently more numerous than the guayule.

PEYOTE (PEYOTL) (*LOPHOPHORA WILLIAMSII* AND *L. LEWINII*).

These cacti are the mescal-buttons or dry whisky of the Texas Indians and cow-men, and have been sought after as the source of a little understood alkaloid of marked effects upon the nervous system. The exposed part of the plant is little more than a convex disk a few centimeters in diameter, of fleshy texture. The stem and root together form a conical, fleshy mass. They are a very modest element in the vegetation, occupying little surface, and may be disregarded from a practical point of view.

There can be little doubt that the component elements in such a vegetation are in a state of ebb and flow, and, in view of the density of the vegetation, in contrast with the condition usually met with in deserts, constitute an important question economically. Here the individuals come into actual contact above ground, where the competition is often severe, as well, presumably, as below ground. Referring especially to guayule, it may be accepted that, when a plant is once well started, it is seldom killed outright by contact with its neighbors, but the occupancy of the ground by other species which have superior methods for spreading gradually reduces the available surface and water-supply for the guayule. This plant takes advantage of surface-water by means of its superficial roots and plants with which it is associated and which behave similarly (e.g., *Jatropha spatulata*) must come into severe competition with it in this regard. But, assuming that, for purposes of forestry, it is desirable to thin out other vegetation in order to favor the guayule, the question arises as to the effect upon the germination of seed of this plant, which is undoubtedly favored by partial shade. It may be argued that the superior numbers of seed available and the shade of the guayule plants themselves will suffice, and this seems probable. On the germination of seed in the open more will be said, based upon experimental evidence (Chapter IV). Denuded areas are under observation, and the future may be expected to bring exact observation to bear upon the practical question of the value of clearing land, as well as upon the theoretical aspect of the questions above stated. (See also Chapter IX.)

#### PARASITISM.

Of vegetable parasites affecting the guayule only two are at present known. Of lesser importance, so far as we may judge, is a rust hitherto known as *Uredo parthenii* Speg. (fig. 5). Prof. J. C. Arthur, to whom material was sent for identification in April, 1908, reports that the fungus properly belongs in the genus *Puccinia*, and may be called *Puccinia parthenii* (Speg.) Arthur, *ined.*, for the purpose of record.

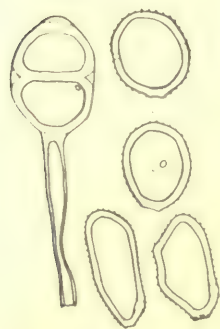


FIG. 5.—Teleuto and uredospores of *Puccinia parthenii* (Speg.) Arthur.

It has been noticed that the fungus appears chiefly on plants which are on the north slopes of arroyos, especially near the bottom, where the relative humidity is most favorable, since it is here that the highest vapor-tension exists. It has been found also on plants growing on ridges, and especially on those which are subject to a condition which we have called "witches' broom," in which the leaves are small and very much crowded. It appeared in the spring of 1908 also on plants which had been grown under irrigation at Cedros, apparently on the older leaves, which still remained attached from the previous year. The parasite is not at all plentiful, and appears to be absent almost entirely from guayule growing in open situations.<sup>1</sup>

<sup>1</sup> A small seedling which germinated in the early summer of 1908 was found in April 1909 with a single infection spot, quite in the open foot-slope (Station 3), in which situation the fungus is seldom seen.

Of more importance, economically, is the "seda" (silk) or dodder (*Cuscuta* sp.), which often grows very plentifully. The habit of this parasite is well known, so that no account of the plant is here necessary. It is very readily recognized as a yellow or orange vine-like leafless organism which winds about the upper twigs and leaves of the host. It is not confined to the guayule, being found also on hojasen (*Flourensia cernua*), on mariola (*Parthenium incanum*), on tatalencho (*Gymnosperma corymbosum*), and other perennial plants, and probably on some summer annuals. It reproduces itself by means of seeds which germinate after the advent of the summer rains, but is to be found vegetating vigorously long before this time. This is explained by the fact that it passes the winter in rather tight, compact clusters of thread-like stems, tightly wound about the uppermost twigs and leaves of the host. (Lloyd, 1908d.) Thus it is independent of seed and is a true perennial.<sup>1</sup>

The effect of the dodder upon the guayule is due to two causes. It diverts water and foods from the host into its own tissues and thus reduces the rate of growth, and it strangulates the twig and leaves upon which it fastens itself. There is thus produced a dwarfing and distortion which is reflected in the whole habit of the plant.

As soon as growth commences in the host, the dodder, which is ready at the top of the previous year's growth to take hold of the new tender tissues, begins to twine about the newly forming stem and leaves and soon overtakes and strangulates them. The effect is to produce very slowly growing plants, and it is seen that the presence of much dodder would materially reduce the annual accretion of growth and therefore of rubber. In periods of severe drought the effect of the dodder is even more marked, since it diverts the already meager water-supply and thus causes the death of the portion of the twig at and above the zone at which the dodder is found. Plants with twigs killed in this way, and in which the dodder itself had succumbed, were found at the close of a sustained drought, in April 1909. The dodder should therefore be stamped out wherever it may be found. The best and only practical means is to harvest with the initial crop all the guayule affected with the parasite. In this way the parasite will be checked, and additional checks will be received at each harvesting by following the same rule.

Indications of another vegetable parasite were thought to be seen in the "witches' broom" above mentioned, but material examined by Prof. W. G. Farlow gave no clue to the cause. The densely packed leaves indeed favor the growth of the rust already described, but this is quite a secondary condition. It is possible that the distortion is due to the cropping of the guayule by animals, but not all plants so treated show it, else nearly all would be affected. Plants closely in the field trimmed back (Station 2, quadrats 1, 2) show a tendency to produce "witches' broom," indicating that constant or close browsing by animals may after all be the cause of this condition.

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<sup>1</sup> *Cuscuta* is sometimes a perennial as far north as the State of New York. Stewart *et al.*, Bull. 305, Agri. Exp. Sta. N. Y., Nov., 1908.



## ANIMAL PARASITES.

The root-system, particularly the tap-root and its larger branches, are frequently found to be infested with two species of the Coccidæ,<sup>1</sup> *Cero-puto yuccæ* (Coq.), and a species of *Orthezia*, distinguishable from the former by the fluted, waxy egg-case attached to the abdomen. The number of these insects found on plants in the field is not inconsiderable, and may be responsible for lesions in the root-tissues which affect the growth of the plant. But of more importance is the circumstance that they occur in greater numbers upon seedlings raised under cultural conditions in wooden trays. Plantlets a few centimeters in height have been found with a dozen or more large individuals on the tap-root, the diameter of which was not as great as the breadth of the mature insects. They may therefore easily be responsible for retardation of growth, though external evidence of lesions has not been noted.

Field plants especially are often infested below the surface of the soil by a scale, identified by Dr. C. L. Marlatt as *Targionia dearnessi* Ckll. This is a widely distributed species in this country. Large tap-roots are frequently half covered by this parasite.

A gall insect attacks the leaves and inflorescence. The female punctures the young leaves and stems, the peduncles, and even the bracts of the capitula, and the resulting galls produce marked distortion. Many of the affected leaves fail of anything approaching normal development; the peduncles are hypertrophied unevenly and become very much contorted, and the inflorescence fails to develop. The net result of the work of this insect is to reduce the rate of growth very materially and to cause a practically complete abortion of the flowers and, therefore, of the seed. The plants affected are readily recognized on account of the irregularity and lumpiness of the terminal growths. The stems proper do not seem to be affected, as the insect appears to commence its work toward the close of the season of growth and to confine itself to the last-formed leaves, which remain attached throughout the winter, and to the inclosed young inflorescences. The increase of growth in the stem is, however, affected indirectly, and the annual accretions frequently amount to less than 1 cm., and scarcely ever to more than 2 cm., during the period of attack. Many plants in circumscribed areas are subject to the attacks of these insects, and it may readily become a serious menace to both the growth of the plants and to their seeding power. The following notes have been kindly furnished me by Dr. Mel. T. Cook:

The study of this material presented many difficulties, as must necessarily be the case when it is not possible to make a field study.

A gall produced by *Cecidomyia parthenicola* on *Parthenium*<sup>2</sup> in New Mexico has been described by T. D. A. Cockerell in *Entomologist*, July, 1900, p. 201. The gall before me does not fully correspond with Cockerell's species, and yet I should hesitate to say that it is an entirely different species without further study, which is impossible with the material in hand. Dissection of the material showed two entirely different species of larva and immature insects, cecidomyid and cynipidous, while a study of the histology presented certain confusing and anomalous characters.

<sup>1</sup> Kindly determined for me by Mr. J. G. Sanders, through the courtesy of Dr. L. O. Howard.

<sup>2</sup> *Parthenium incanum*, presumably.

The isolated galls were small, monothalamous, and in the shape of a truncated cone, usually on the upper surface of the leaves and standing in an oblique position. The opening of the larval chamber was through the top and was guarded by hair-like growths or trichomes, which pointed inward. This would indicate a cecidomyid gall, but certain preparations showed the opening closed by a thin membrane. Whether this latter condition was real, therefore proving the presence of two species of galls, or only apparent, was difficult to determine, owing to a tendency of the galls to coalesce, forming irregular masses.

## HISTOLOGY.

The gall in its earliest state shows the reduction of the palisade into cells of the mesophyll type. This condition is characteristic of the origin of all leaf galls. As the gall develops, the cells, which constitute the lining of the larval chamber, are rich in protoplasmic content, which decreases from inner to outer surface. This is indicated very readily by the stains and is characteristic of the more highly developed galls and usually designated as the nutritive zone. A little later certain galls showed a reduction of the nutritive zone and the formation of a protective zone of sclerenchyma cells just outside the nutritive zone. The presence of this protective zone is characteristic of the galls produced by cynipidous insects, and the writer has never found them in galls caused by cecidomyid insects.

From the above facts, it appears that we may have two species of galls, one produced by a cynipidous insect and the other by a cecidomyid, or a single gall which has been parasitized.

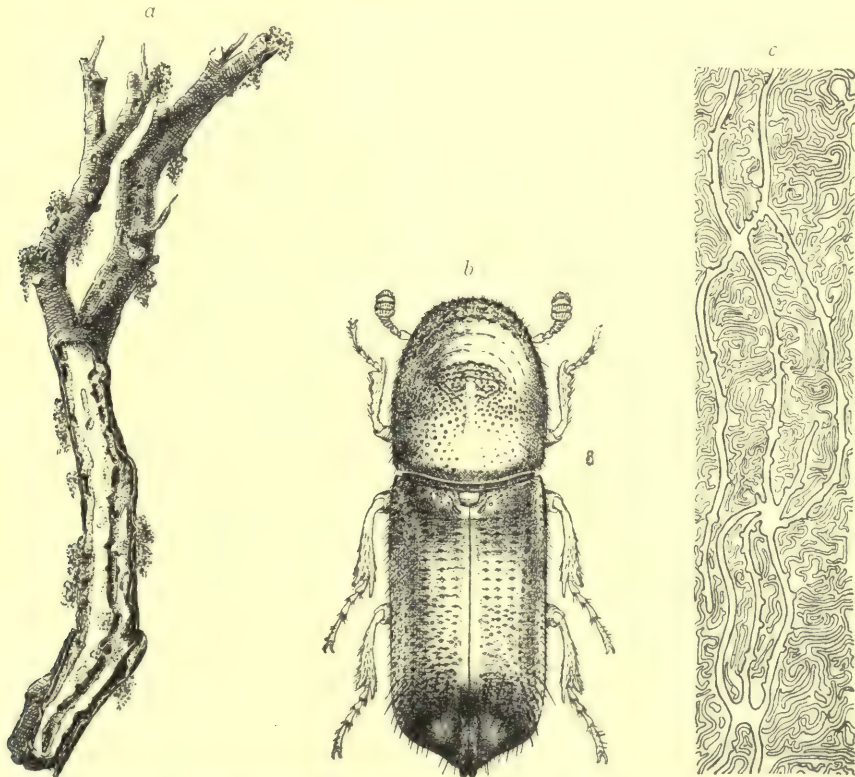


FIG. 6.—The guayule barkbeetle (*Pityophthorus nigricans* Bland). (a) Work of beetles and larvae in bark and wood. (b) Adult beetle, greatly enlarged. Small figure at right shows natural size. (c) Egg-galleries of parent beetles, with intervening larval mines, all grooved on surface of wood. (From illustrations loaned by the Bureau of Entomology, U. S. Dep. Agric.)

## THE GUAYULE BORER.

In the fall of 1907 it was noticed that guayule in the stack (plate 4, fig. A), awaiting treatment for the extraction of the rubber, was being attacked by an insect, the only signs of which were the finely-powdered débris escaping from minute, circular openings in the bark. It was at once evident that a borer of some kind was at work. Material was sent to Dr. L. O. Howard, who kindly referred the matter to Dr. A. D. Hopkins, in charge of forest insect investigations, Bureau of Entomology, U. S. Department of Agriculture, to whom I am indebted for the accompanying notes and drawings (fig. 6, p. 43). Dr. Hopkins writes as follows:

The beetle is *Pityophthorus nigricans* Bland. It has also been reported to the Bureau of Entomology by H. Pittier, who found it injuring the same plant at Torreón, Coahuila, Mexico. The insect is of special interest because of its habit of attacking a plant of such commercial value, and on account of its being the largest representative of the division of the genus to which it belongs. Those of one division infest coniferous trees only, while those of the other, to which this species belongs, infest only the broad-leaved plants and trees. The guayule barkbeetle evidently attacks the plant after it is dead, or soon after it has been cut, and, as has been shown by the specimens in the forest-insect collection of the Bureau of Entomology, may continue to breed in the same bark and wood for several years. It is evident that the prompt utilization of the plant for the manufacture of rubber within a few days after it is cut would prevent all losses from this source.

Inasmuch as the buyers of shrub sometimes accumulate large quantities and place it in stacks until needed, and as this may represent large investments, the amount of damage may represent no inconsiderable loss. In order to determine what this loss might amount to, a piece of stem of average thickness which had been attacked by the borer was weighed as a whole. It was then decorticated and the insect débris was carefully removed. Some of the débris had of course been lost, and thus an error is introduced into the calculation of fully 5 per cent of the total weight of the bark. The tunneling done by the insect was not complete, however, and for this reason the figures may be regarded as the average result of the damage which may occur in the space of a month or two.

TABLE 19.

	mm.		grams
Length of sample piece of stem.....	25.	Weight of the whole.....	3.801
Diameter of the wood.....	9.8	Weight of wood cleaned of débris.....	1.703
Thickness of the bark.....	2.3	Weight of bark cleaned of débris.....	1.903
Total diameter of the stem.....	14.4	Weight of material lost (with probable correction).....	0.2
		Of which half is bark, viz.....	0.1

It can be mathematically shown that the amount of destruction in the smaller twigs in which the insects work may amount to very considerably more, indeed to the extent of 40 per cent of the volume of the bark (cortex). Inasmuch as the bark contains practically all the rubber, it is seen that the loss may be great enough to warrant serious consideration. It must be observed, however, that the comminution of the cortical tissues by the beetle does not diminish the amount of rubber in the stem except by the amount that happens to escape through the entrances, so that the real question is, whether the comminution of the cor-



tex and of the rubber contained in it renders the rubber unavailable in the manufacture of the crude product or not. In order to answer this question, a sufficient quantity of the *débris* was collected and subjected to mastication. By this means it was possible to cause the partial agglomeration of the rubber, but it was quite impossible to separate out the "bagasse" on account of the fineness of the particles. These have the effect of separating the rubber so that it is in the form of a fine mesh-work, the connecting isthmuses not appearing to be great enough to overcome the surface-tension of the smaller masses. Microscopical examination shows the mass to be composed of minute fragments of tissue derived from the wood and cortex embedded in the rubber. Measurements of these particles showed them to be 0.02 to 0.1 mm. in size, occasional pieces being as large as 0.5 mm. If during mastication one is careful to allow only a small amount of saliva to bathe the mass, it may be held together for some time, but if it be flooded for a moment and worked meanwhile, it will quickly disintegrate and can not be reagglomerated. It therefore appears that the work of the beetle, while not destroying the rubber, puts it into such condition that it is lost to the manufacturer who uses a mechanical method of extraction, since the minute particles can not be made to agglomerate. When the insects have once got a fair start in a stack-yard the amount of damage which may be caused in a short time by their very large numbers may be great enough to warrant the adoption of means to avoid the loss, if it is found that stacking the guayule is necessary.

#### CROPPING BY GRAZING ANIMALS.

It has been pointed out that the growing guayule is browsed by animals. Burros, jack-rabbits, cotton-tails, and goats are all given to this, and as these animals are numerous a great loss is entailed. Goats are herded habitually in the guayule fields, and these animals, with their all-devouring appetites, eat almost everything that grows. Not the least damage done by them is the wholesale destruction of the developing shoots and flower-buds, reducing the crop of seeds very greatly. Goats and burros may, however, be pastured away from the guayule fields, and thus loss may be avoided.

The work of rabbits, where other food is available, is not serious, though in the event of adopting forestry methods they may become a menace to the plant. These marauders do not merely crop off the foliage and new shoots; they lop off whole branches, which are left on the ground to die. One jack-rabbit may therefore do a great deal more damage than a goat in the same time. It has been noticed that they treat the *gobernadora* in the same way. One frequently sees a complete circle of dead branches about the base of a bush, all having been lopped off at one time.

# CHAPTER III.

## DESCRIPTION OF THE GUAYULE,

*Parthenium argentatum* Gray.

### SEED.

The word seed is here applied in a loose sense, inasmuch as the body to which the term is applied is, correctly speaking, an achene, a one-seeded fruit in which the pericarp remains indehiscent and dry. What passes as "seed" in guayule is a mixture of achenes, sterile flowers, involucre scales, and pedicels, and, inasmuch as the opportunities for sophistication are nearly always at hand, and for the reason that the peon employed for the gathering of seed will not always be diligent in distinguishing between guayule and mariola "seed," the present chapter may appropriately begin with a description of the flower.

In the genus *Parthenium*, as in all the Compositæ, the order to which it belongs, the flowers are arranged in heads or capitula (fig. 10). In the

guayule these are about 5 mm. in diameter, and contain two kinds of flowers, commonly known as ray and disk flowers. The rays are normally five in number, and are readily recognized during flowering by the open corollas, which project radially beyond the margin of the capitulum. These only produce seed, each a single one, if fertile.<sup>1</sup> The disk flowers produce pollen but are incapable of setting seed, although the pistil is present and serves after the fashion of a piston

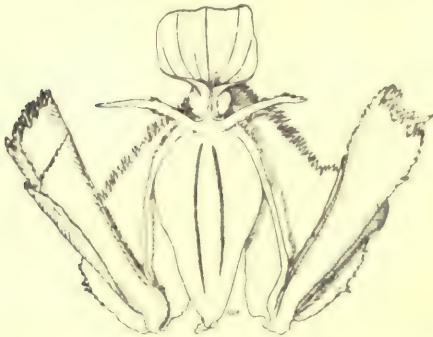


FIG. 7.—Ray-flower with attached disk flowers and the subtending bracts. *Parthenium incanum*.

to eject the pollen, as commonly occurs in the Compositæ. When the fruit is ripe and the period of flowering is quite past, the capitulum becomes dismembered in a somewhat unusual fashion. Each ray-flower, the two adjacent disk flowers and their subtending involucre bracts, become attached to each other by concrescence, and fall away as a whole (fig. 7). The remainder, i.e., all but ten of the disk flowers, also remain attached to each other and fall away as a shriveled, conical mass. There remain behind five involucre bracts persistently attached to the receptacle which supported the whole. In collecting "seed" all of these are taken, so that it will be seen that the bulk of the material is chaff.

Considering the fertile flower and its accompaniments, we observe that the achene is hidden between the adjoined pair of disk flowers and its own bract. This bract, which is quite broad and concavo-convex, is

<sup>1</sup> Polyembryony occasionally occurs.

composed of three morphological elements, fused above, but more or less loosely connected below; a rare occurrence, analogous to the condition of some stamens. The middle element is the narrowest, and is the bract proper of the pistillate flower. This, to be seen, must be dissected out.

Another peculiar feature then becomes apparent, namely, that the two disk flowers can not be separated from the achene without pulling away two narrow strips of tissue from its margins. (Fron et François, 1901.) The whole arrangement would appeal to the teleologist as an excellent adaptation for dissemination by the wind or by water, since the thin, light, and air-imprisoning tissue may serve as wings or floats according to circumstances. The achene itself is crowned by the persistent but shriveled corolla, and at either side of this and against its ventral (upper or inner) aspect are three short awns,<sup>1</sup> one in each position. The achene proper is ovate, with an acute base. It is partially clothed with short appressed hairs, but for which the pericarp would be black or dark gray. The achene measures 2.5 mm. in length by 1.8 in breadth when of normal size, exclusive of the awns.

The "seed" of the two other species, mariola (*P. incanum*) and *P. hystrophorus*<sup>2</sup> (an annual), which grows with or near the guayule, may be distinguished by attention to the character of the lateral awns, which may readily be seen with a lens by viewing them as they project beyond the bract. In the guayule the awns are brown, with papery, denticulate margins. In the mariola these are slender, appearing denticulate or quite without membranous margins, tapering and distinctly reflexly curved, and are usually darker in color, being black toward the

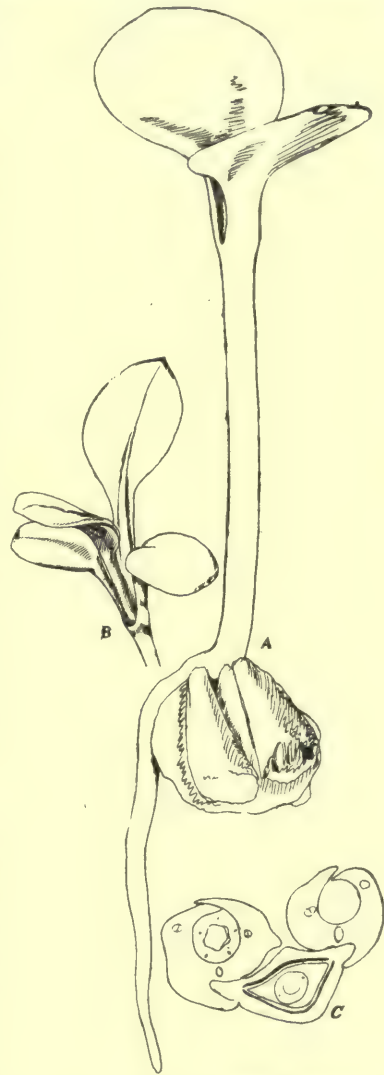


FIG. 8.—A, a fully germinated seedling of guayule, before induration,  $\times 8$ ; B, cotyledons and first two foliage leaves; C, transverse section through achene of a ray flower and its two attached disk flowers.

<sup>1</sup> Taxonomic works usually indicate that there are only 2 awns, but this is an error. There are 3 awns in *Parthenium argentatum* and *P. incanum*; 2 in the herbaceous *P. lyratum* and *P. hystrophorus*. Engler and Prantl describe the genus as having 2 to 3 awns, but do not indicate further details.

<sup>2</sup> This plant grows in great profusion in the summer months in the alluvial plains upon which the guayule lands border.



base. In *P. hysterothorus* and *P. lyratum* they are very broad, and are membranous in the former. Figs. 7 and 9 will make these and other characters evident.

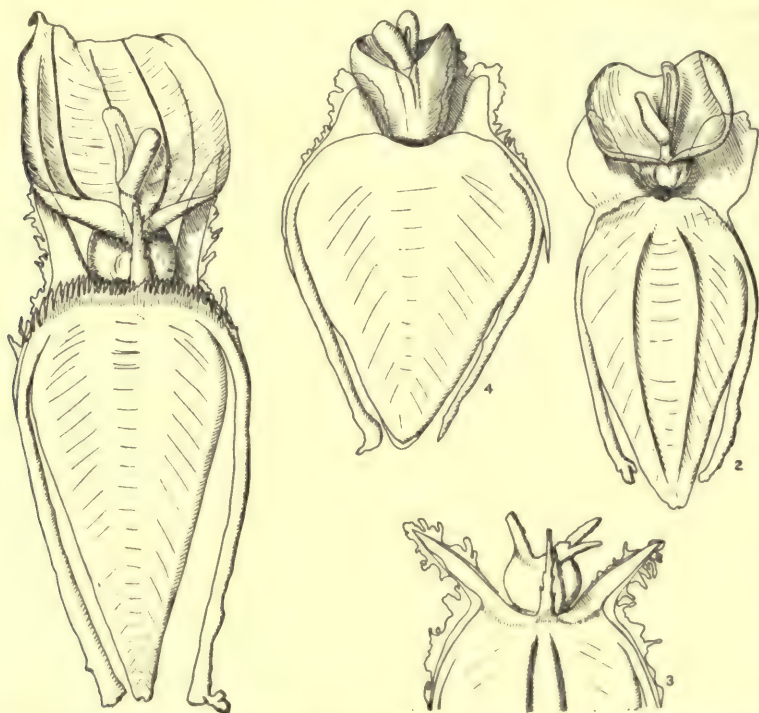


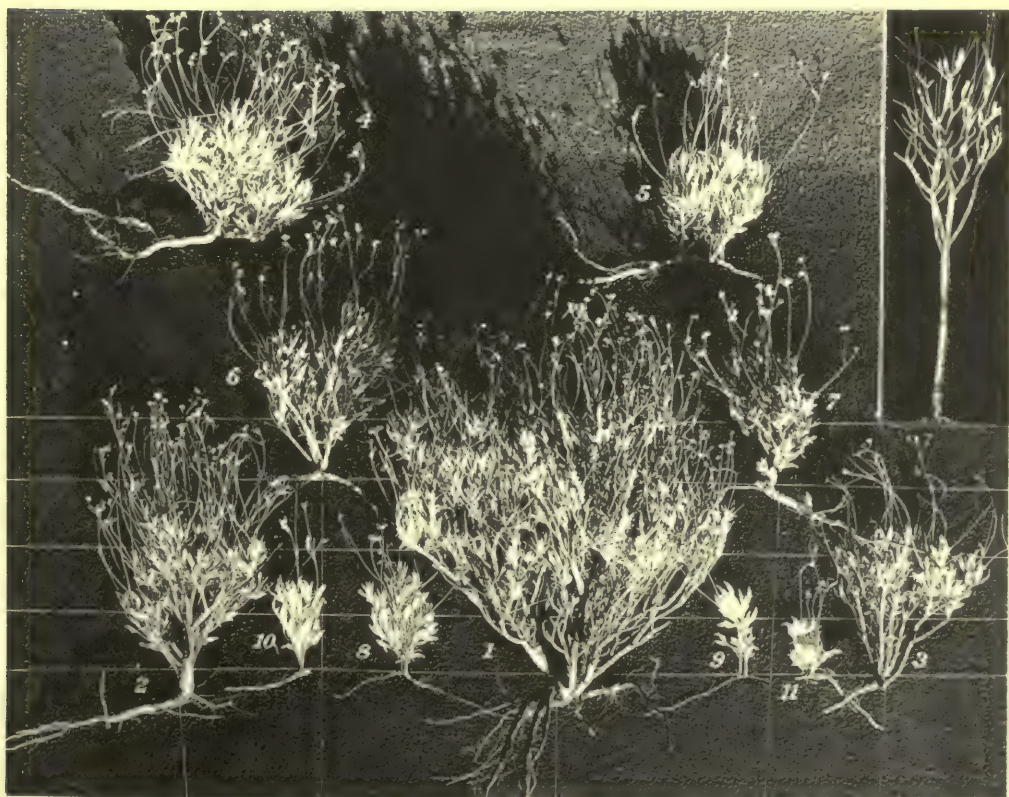
FIG. 9.—Achenes of (1) *Parthenium argentatum*, (2) *P. hysterothorus*, (3) *P. incanum*, (4) *P. lyratum*.

### SEEDLING.

When germination is complete the seedling of the guayule consists of a short primary stem (hypocotyl), 5 to 10 mm. in length, terminating in a long, slender tap-root. Attempts to find the end of this in the field have been fruitless, on account of the nature of the ground and because of its very tender character and great length and thinness. Experiments show that it reaches a depth of at least several inches. This slender rootlet, with very few branches, is the means of keeping the plantlet supplied with water from the soil for some months, as frequently during the first year in the field no adequate development of lateral roots occurs. The seed leaves (cotyledons) are nearly or entirely circular in form, and range in size from 2.5 mm. in width by 3 mm. in length to 4.5 mm. in width and 4.7 mm. in length, according to various conditions. At the apex of each cotyledon is a hydathode, composed of a group of water stomata. Other conditions being the same, seedlings grown in the shade and high relative humidity have the largest cotyledons (plate 34, figs. 6, 9), and the largest were seen on seedlings grown experimentally under such conditions. The primary stem is about 1 mm. in diameter, and in seedlings grown under natural conditions, *i.e.*, with direct sunlight, is dark red; in



A



B



C

- A. The root-system of guayule.  
 B. Group of plants which started as retoños.  
 C. A strongly monopodial retoño.





shade plants it is green. The dark-red color extends also over the under surface of the cotyledons, which are rather thick in sun forms, and thinner in shade-grown plantlets (plate 34, figs. 4, 6).

The early foliage leaves, soon after germination and because of the very short internodes, are closely crowded. By partial etiolation these internodes may be caused to lengthen, and thus the structure of the primary epicotyledonary stem may be better studied. In this way points may be made clear which otherwise would with difficulty be explained. The first 8 leaves are usually ovate, entire, slightly acute, and taper suddenly into the petiole (fig. 8). They are clothed, as are all the foliage leaves, with closely set T-shaped hairs (plate 30, figs. 9-11) laid parallel to the axis of the leaf, and thus is produced that light green-gray, satiny sheen which characterizes the plant. The first leaf is usually about 1 cm. long by 3 mm. wide, though measurements vary a good deal. In the mariola seedling the earliest leaves resemble those of the guayule, but differ in being broader and lanose, a difference due to the form of the trichomes, those of mariola being of the "whip" form found frequently in the *Compositæ*. As the hairs are much thicker on the under side of the leaf, the species may be very readily recognized even when only one foliage leaf has developed, though identification is difficult before this leaf appears.

The last formed of the entire-margined seedling leaves may reach, in field plants, a length of 7 to 8 cm. and a width of 1.5 cm. The first approach to the mature leaf form is seen in a single tooth, usually on one margin only, at about the middle of the blade. In the next stage the tooth may be found on both sides, and larger, while half-way between their position and the apex a second pair of teeth appears. By basal contraction of the blade and extension of the upper portion, the first teeth appear to move downwards, and by enlarging attain lobate proportions. The leaf is now relatively shorter and broader. An additional pair of basal teeth may also add to the complexity. While this description, illustrated well in plate 18, is generally true, few plants are more variable as regards the form of the leaf than the guayule, and this variability is, with the exception of the earliest foliage leaves to be formed, closely connected with the amount of available soil-water. Thus we find that in plants grown under irrigation the amount of lobing is very much more marked than in field plants. We shall return to this subject later.

The first inflorescence is usually formed early in the history of the plant, and may occur in the first growing season even in field plants, though this is exceptional (plate 17). This early flowering in a shrubby plant of long life appears to reflect its relationship to herbaceous forms, and would not improperly be regarded as indicating that the perennial habit of the guayule and mariola is, phylogenetically, a recently acquired character. The inflorescence, which is a compound monochasium (fig. 10), is terminal, and thus ends the growth of the chief shoot. In some instances flowering may not occur for some years, and in this event if no accident befalls the chief shoot it may attain a length of 15 cm. or more before the first flower shoot appears to conclude the growth of the chief axis. In such a case the lateral shoots make but little growth. Upon the first occasion of flowering the growth of the branches begins; these

in turn terminate in inflorescences and, by ending their growth, give stimulus to the growth of branches of higher orders, each in its turn. Thus the plant becomes profusely branched, and this habit contributes materially to the amount of secretion, which is proportional to the number of branches.



FIG. 10. —The inflorescence of the guayule.

## THE MATURE PLANT.

### ROOT-SYSTEM.

The root-system of the guayule consists, in a plant derived from a seedling, of a strong tap-root extending to a considerable but undetermined depth in the soil. The lower end, which branches more or less, draws upon the water-supply of the deeper layers of the soil, especially in younger plants. Just below the surface of the soil a number of strong lateral roots are given off, which in many instances are of extraordinary length, reaching a distance of 150 to 200 cm. or more from the plant (plate 9, fig. A). These serve to take up the water in the shallower layers of the soil, derived from rains sufficient to wet the soil to this depth. Such far-reaching, shallow-placed roots are characteristic of many desert plants. Cannon (1909) has studied and mapped the root-systems of a number of such, and has further shown that competition between juxtaposed plants may be eliminated by the difference in the type of root-system, the one going deeply, while the other is chiefly shallow. The development of two differently placed parts of the same root-system, the one drawing on the deeper, the other on the shallower layers of the soil, is of very great importance biologically, and is well exemplified by the little cactus *Ariocarpus kotschubeyanus*, which grows in the alluvial plains of the *mesa central*. The shallow roots arise from the top of the tap-root and ascend as nearly vertically upward as may be, till they reach to within a few millimeters of the surface of the soil, when they suddenly take a hori-

zontal position, and in this direction traverse considerable distances from the plant. This condition is closely analogous to that in the guayule and serves to make even clearer the significance of the arrangement in that plant and in others, in all of which the tap-root system, while quantitatively inferior both as regards the number of branches and the amount of water absorbed into the superficial system, may nevertheless be of a good deal of importance in enabling the plant to withstand prolonged drought when the shallower portions of the soil become very dry. This is indicated by the readiness with which retoños arise from the tap-root after the plant and lateral roots have been cut away.

#### RETOÑOS.

From these shallow lateral roots there frequently arise new adventitious shoots, sometimes singly, sometimes in groups of two or more (Lloyd, 1908c) (plate 9). They are locally called "retoños," though this term is not always used strictly, and may apply to shoots arising from stem tissues. It is the same word as "ratoon," used by sugar-cane planters, but as this is used constantly to indicate offshoots from the base of the stem, it is inapplicable as an equivalent of retoño. Since it is the only term used in Mexico for these shoots of root origin and as our common English equivalent is characterized chiefly by its inelegance, we shall venture to retain the Mexican-Spanish expression.

Retoños usually arise from the plant at a distance of 20 cm. or more. They have been found at a meter's distance, and doubtless may occur still further away. The point of origin may be above, below, or at the side of the root. As growth proceeds the proximal part of the root fails of further secondary thickening, or at most undergoes very little thickening. It ultimately becomes abstricted by decay, apparently induced by pressure of the tissues of the retoño, and quite soon loses its physiological value. The distal portion, however, thickens more rapidly, keeping pace with the growing retoño, and takes on the proportions of a tap-root, though it may always be distinguished from a true tap-root by its curvature and position in the soil. Secondary, adventitious roots (fig. 11) later arise from the basal portion of the stem of the retoño, thus amplifying the root-system. A large root-system thus developed is shown in the central and largest plant in plate 9, fig. B.

The author of this publication stated as follows in a previous paper :

The formation of these new plants in this manner is not spasmodic or exceptional, nor are they fugitive in their nature. Under certain conditions they are produced in such numbers as to entirely overshadow the numbers of seedlings; and they as frequently grow into maturity, producing a plant which, if the origin were not known, would not unlikely be considered a varietal type, in point of habit. The mature plant which had its origin as a seedling has a single trunk, usually 10 cm., sometimes 20 to 30 cm., in length; the mature plant produced vegetatively has usually a very short trunk, or a group of separate ones, more or less coalesced by growth, though marked exceptions may occur (plate 9, fig. C).

The ratio of the number of new plants arising as seedlings and of those arising as root-shoots varies with the habitat. Both forms may be found in any situation, but the retoños are much more numerous on stony slopes, often outnumbering the seedlings. The reverse relation is seen in more level places. Thus, at the foot of a low ridge I have found seedlings plentiful, as many as 30 in a square foot (these small and larger ones as well scattered about relatively thickly). A zone of this



character could be traced around the ridge. Just above this zone another could be made out in which the retoños were abundant and the seedlings scarce, while coming to the top of the ridge the seedlings again outnumbered the retoños. Thus on that part of the slope most affected by erosion, and where there is more chance of uncovering the shallow roots, the retoños are most abundant. It would appear, therefore, that the exposure to light is a potent, if not the most important, factor in inducing budding in the roots. Yet I have found that when a plant is removed by cutting at the base so as to sever the roots and leave them in the ground, shoots start from the root, not only where the root is accidentally exposed, but as far back as the drying out of the root makes it necessary. A root thus severed in January failed to bud till June in consequence of the lack of rain; when at last it rained, the buds started out 12 cm. away from the cut end and several centimeters deep in the soil. On the other hand, roots purposely exposed for a portion of their length and slightly wounded had failed to start buds at the end of six months when last examined.<sup>1</sup> So the case appears to be more complicated than at first appears. Injury may be a factor at times, but, experimentally, I have shown that scarring or cutting the cortex is not sufficient to insure budding, at least under field conditions, for it is probable

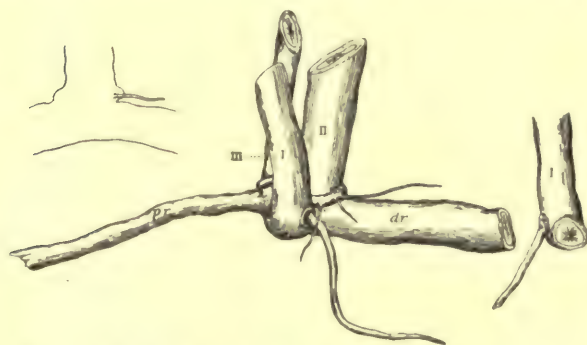


FIG. 11. Retoños, showing position of adventitious roots. *pr.*, proximal portion, and *dr.*, distal portion of mother-root.

that the exposure to a low relative humidity inhibits the growth of callus on exposed roots. It is more probable that had roots been injured and left covered with soil, positive results would have accrued.

This occurrence of retoños in guayule presents a very interesting biological phenomenon. In a habitat where the rainfall is very meager, so that years occur in which the conditions for germination are prohibitive, and where, moreover, sudden and severe rains wash the soil

on the steeper slopes severely enough to remove seeds or expose seedlings when young so as to prevent their further growth, it will easily be seen that the vegetative method of reproduction presents certain very marked advantages. This is true also where the soil is confined to the crevices of the native rock where it lies at or very near the surface. This condition occurs very frequently in North Zacatecas, where large areas will be seen in which the vegetation is confined to bands of outcropping rock, where it occupies the soil beneath the edge of a stratum. Where the relation of the strata to the surface is such that flat blocks of rock support but a thin layer of soil, the distribution of vegetation is determined by the fissures. In the case of guayule we have an exception, for this plant may send out a shallow lateral root over a block of stone, above which plants may start. Very frequently we find individuals which have grown in this position, with their roots straddling the sub-imposed rock. Such are almost invariably retoños. Plant 1 (plate 9, fig. B), was found so placed. There are other plants which can compete with the guayule in this regard, such as the lechuguilla (*Agave lechuguilla*), which spreads out by means of stolons, and occupies areas for itself to the exclusion of everything else. It is clear that the habit described is of no small importance in the fight for foothold. One can easily imagine, too, that a distinct advantage is to be had in the rate of growth and the quickness with which the ability to flower abundantly is reached by retoños. The rate of growth is relative to the size of the mother root; but it is a very common thing for a retoño to grow 10 cm. and to come into flower in two months in summer (plate 9, fig. B, 10 and 11). Seedlings, on the other hand, flower only

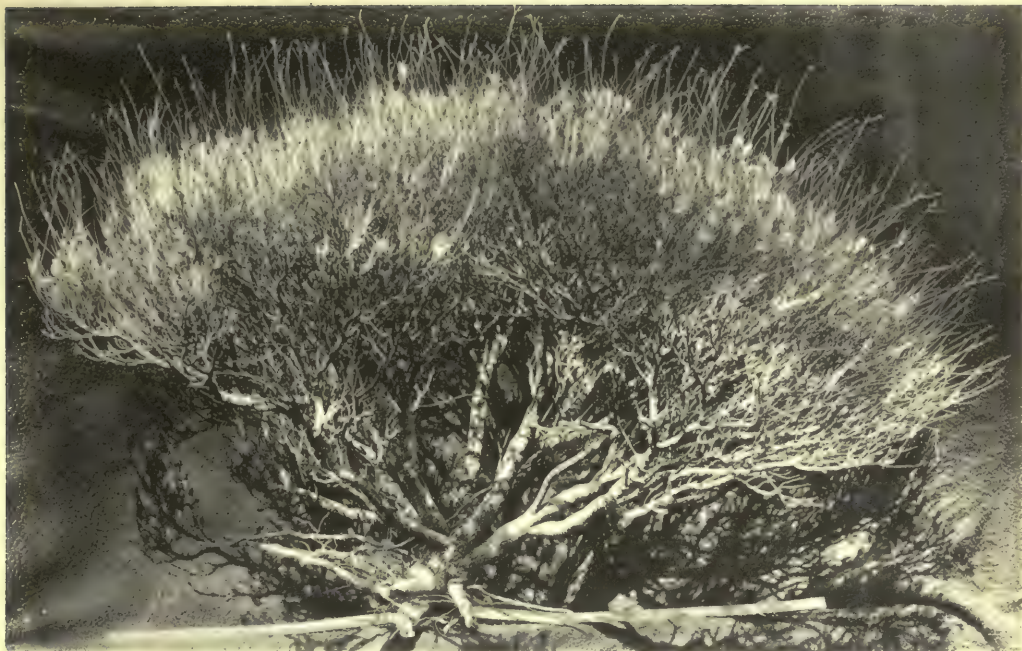
<sup>1</sup> Only negative results were had as late as September 1908.



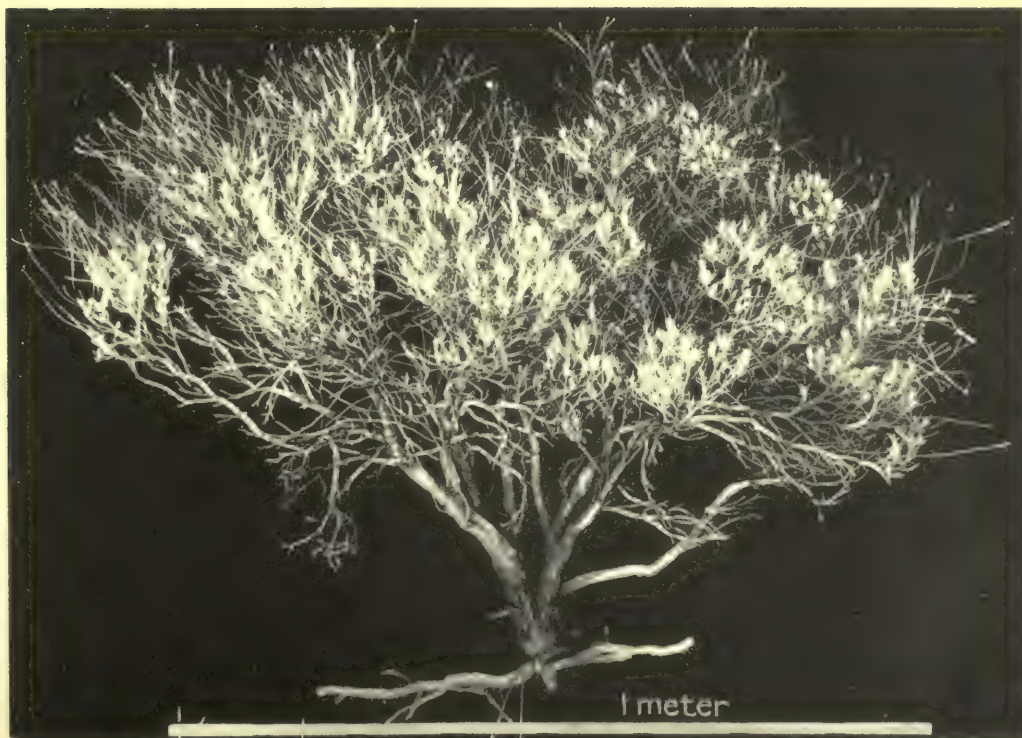
An exceptionally tall (130 cm.) individual. Weight 9.4 lbs. Caopas.







A



B

- A. A widely spreading (130 cm.) plant of guayule. Weight 10 lbs. 9 oz.  
B. A large plant of the usual habit. Weight 8.5 lbs. Apizolaya.





A biotype of guayule. The winter condition on the left.





infrequently before the third year, and the amount of growth then does not more than equal that of a single-stemmed retoño in one year. At the end of three years the retoño makes a considerable plant (6 in the same plate), and flowers richly. The influence which retoños would have in reforesting processes, both by their own growth and by seedlings, can therefore be well appreciated, and probably with difficulty overestimated. Some basis for judgment in this regard will reward a study of the accompanying photograph<sup>1</sup> (plate 9, fig. B, in which the horizontal lines are to be regarded as 10 cm. apart).

From his comparative morphological and anatomical studies on "normal" parts and those of individuals ("rejets") arising from root buds, Dubard (1903) draws the following conclusions:

En résumé, la multiplication par bourgeons radicaux est un fait peu normal dans le règne végétal; elle donne naissance à des rejets d'organisation inférieure, dans la plupart des cas; chez quelques espèces elle tend à s'établir d'une façon régulière, mais ne devient qu'exceptionnellement une sauvegarde effective de l'espèce.

The inferior organization of the retoños studied by Dubard is always in the direction of an anterior form "by virtue of hereditary antecedents": "les rejets radicaux des diverse espèces d'un même genre manifestent une convergence qui ne peut être fortuite."

The retoños of the *guayule* are in the same case. The absence of medullary and of cortical canals is a marked return to a more simple structure, as is also the absence of medullary stereome, in which, and in the absence of canals in the medulla, we see an assumption of seedling characters. But the retoño assumes a still more ancient condition, we may believe, in the loss of the cortical canals.

Nevertheless, the *guayule*, while in this measure conforming to the observations made by Dubard, can not on any account be relegated to a subnormal category, characterized by comparative impotence in safeguarding the species. The frequently strong vegetative growth; the early maturation of flowers and seeds; the already established root-system; the cincture of the mother root tending to separate the retoño physiologically, if not always structurally, from the parent plant (fig. 11); its frequently wide separation from this; its ability to gain a foothold where seedlings must surely perish; all these facts heighten the importance of the retoño, despite the relatively small numbers in which they are found, in enabling the species to maintain a foothold. It seems, indeed, not unlikely that a further classification beyond that of Dubard will be necessary—one for those plants in which the retoño is of great importance in this regard.

A comparison at this point between the *guayule* and the *mariola* is of special interest, because, while they are closely related species, their methods of vegetative reproduction are quite distinct.

In the first place, the root-system in the *mariola* differs in that the laterals run at a steeper angle into the soil. Occasionally retoños are formed, but, as far as my observation goes, always close to the plant, within, say, 5 cm. What always happens, however, is this: From the basal portion of the stem, where there are many dormant buds, as a sequence of the short internodes marking the slow initial growth of the seedling, new, slender shoots arise, growing to a height of 30 cm., more or less, in two months. From the base of each such shoot an adventitious root starts out, immediately above the point of origin of the shoot. This usually single root develops as a tap-root, and supplies all the water for the daughter shoot,

<sup>1</sup> F. E. Lloyd, 1908c.

which develops apace, and ultimately becomes an independent plant. The isthmus of tissue between it and the parent plant does not enlarge much in any case, so that it is quite easy, on taking up a bush of mariola, to separate it into several smaller plants by merely breaking off the functionally independent elements. Thus the habits of mariola and guayule in this regard are so different that one plant, the former, remains a single-stemmed shrub of tree-like habit, while the mariola is of the bushy habit. This marked difference, it will be seen, precludes the advisability, though the possibility might remain, of grafting the guayule on the mariola, a suggestion which has been made on the assumption that increased growth might follow in the scion. No economic result would follow, and for this reason: Suppose that we successfully graft a piece of guayule on a stock of mariola. The scion grows, but at the same time new shoots arise from the base of the stock as described, and their growth is so rapid that in a month or two the guayule shoot is overtopped, and this ends the usefulness of the graft for economic purposes. We might very well make a graft for the purposes of pure science, but economically it would be a failure (Lloyd, 1908c).

Recently it has been proposed (Escobar, 1910), but with admirable reserve, that the dissemination of guayule seed in areas where only mariola grows may be attained by grafting guayule upon it. The plan appears impracticable.

#### METHOD OF BRANCHING.

It has been pointed out above that the monopodial growth of the seedling is brought to a close by the development of the first inflorescence. Following this event, several of the uppermost branches make a more rapid growth. These branches in turn end their growth each by the formation of an inflorescence, when usually the two or three uppermost buds continue to lengthen. Thus is produced a constantly divaricating system of stems (plate 11, fig. A), which, if uninjured, results in a splendidly symmetrical and closely branched shrub. A very exceptional plant, approaching the ideal form, is seen in plate 11. Through failure of some branches to develop, irregular forms are often seen. These usually attain a greater height than the symmetrical plants. An unusually tall plant is shown in plate 10, in which the irregularity of growth is illustrated, while in plate 11, fig. B, a form more frequently met, especially in very rich fields, is shown.

A comparison with the mariola is here pertinent, as there appear to be two types of guayule in respect to the manner of branching, one of which approaches the condition in mariola. The usual manner of extension of the branching system is by the nearly equal growth of two or three branches just below the inflorescence (plate 14, fig. B). As will be seen, the anatomical distinction between stem and peduncle is abrupt, and the dead and, according to age, more or less disintegrated peduncle remains as a spur in the angle between the uppermost branches. Often this may still be seen after the lapse of many years. No absciss layer is formed,<sup>1</sup> and this again gives a suggestion of the recent departure of the shrubby type from the herbaceous ancestor. After flowering, the dead peduncles remain in evidence above the foliage of the plant and form a conspicuous character. In the mariola, on the other hand, with the same morphological basis, a different habital form is had. The stem, as in guayule, ends in an inflorescence, is more slender, and is beset with short branches or

<sup>1</sup> This condition is, of course, common to many plants, and is specially prevalent among the Compositæ.



spurs, which, because of the more rapid growth of the shoot in mariola, are more numerous developed. The transition into the peduncle is gradual, and not sudden, as in guayule; this organ is, therefore, not sharply delimited, either morphologically or anatomically, and is leafy and provided with buds well up beneath the inflorescence. In the following growing season, and this usually means in the following year, some of the short spurs develop into leafy branches and in their turn terminate in peduncles. These, like all the branches, are slender and tapering, and their position, rate, and manner of growth result in a close interweaving of stems, in striking contrast with the guayule.

#### BIOTYPES.

Returning to the subject of habitual types in the guayule, it has been found that some plants have the mariola manner of growth (plates 12 and 13). Instead of an abrupt termination of the stem at the base of the peduncle, the transition is gradual and the stems are of smaller diameter than in the usual type. Foliar differences are to be noted beyond. The matter is possibly of practical importance, as the slender branches with vaguely delimited flower-stalks would, *mutatis mutandis*, contribute to produce a less desirable form of plant from the point of view of production. A phylogenetic interest also attaches to it, inasmuch as the mariola habit is more closely comparable to the herbaceous manner of growth, as displayed by congeneric herbaceous species, than is the guayule habit. On this score, as on others, the guayule is the type more widely divergent from the theoretical herbaceous ancestor.

These differences are, indeed, quite fundamental, and may be traced back to the earliest seedling stages (plate 13). The clearness of the distinctions is such as to indicate that we are dealing with a field mutant, and the differences in the structure of the awns (pappus) would seem sufficient ground, in the light of the taxonomy of the genus, to warrant us in regarding the broad-leaved type as a distinct species. The two forms, *P. argentatum* proper and this closely related form, be it a well-marked species or a type of less taxonomic evaluation, are remarkably distinct, and call to mind many similar juxtapositions of closely related species, recognized as such, known to occur among plants, but not yet properly appreciated as evidence in the discussion of isolation (Lloyd, 1905b).

Another difference in the habit—though not correlated, it appears, with the manner of development of the inflorescence—is seen in what may be termed straight and crooked limbed forms. The one is clean-cut and smooth-limbed, each span of growth being nearly straight; the other is rougher barked, the more slender limbs showing marked curvatures. The former is the more rapidly growing type, suggesting differences in the available water-supply. One frequently finds examples of very marked growth differences in field plants, such as are shown in plate 9, fig. A, of which the right-hand plant grew in a shallow rock crevice and was unable to develop a competent root-system. The annual accretions of growth in this plant were very short, not exceeding a centimeter, and this resulted in the production of a very dense, much-branched mass of limbs, as seen in plate 9, fig. A, on the extreme right. This and

the left-hand plant in the same figure show extremes of rate of growth, somewhere between which lies the average, which it is desirable to know in estimating the rate of reproduction.

A still further difference in habit, which is not very readily distinguished from the foregoing at first glance, is one recognized by persons engaged in the gathering of the shrub, who designate the two types in question "macho" or male and "hembra" or female. The differences, which are shown in plate 14, fig. B, were pointed out to me by Don José Herrera, a gentleman who has had a great deal of practical experience in collecting shrub. "Macho" guayule has fewer branches, and they have a larger diameter than those of the "hembra," in which the branches are much more numerous. These terms are not here used in the sense spoken of on page 4, to distinguish guayule from mariola, which latter is sometimes called "hembra de guayule," but merely to designate the plant with the stronger and therefore "macho" habit and that with the weaker or "hembra" habit. These adjectives are used analogously with respect to other plants showing similar differences. "Hembra" guayule makes greater bulk when made up into bales, and for this reason those who gather shrub prefer to take it if they are being paid at a rate per bale. Whether the differences are biotypic or are due merely to environmental conditions can not be said; nor whether there are other correlated differences, as in the amount of rubber secreted, though such are variously claimed to obtain. There appears to be a stronger tendency in the "hembra" for the branches to run out into inflorescences, entailing a greater amount of dying back at the close of each growing-season, and thus it may turn out that these differences are essentially the same as those mentioned previously.

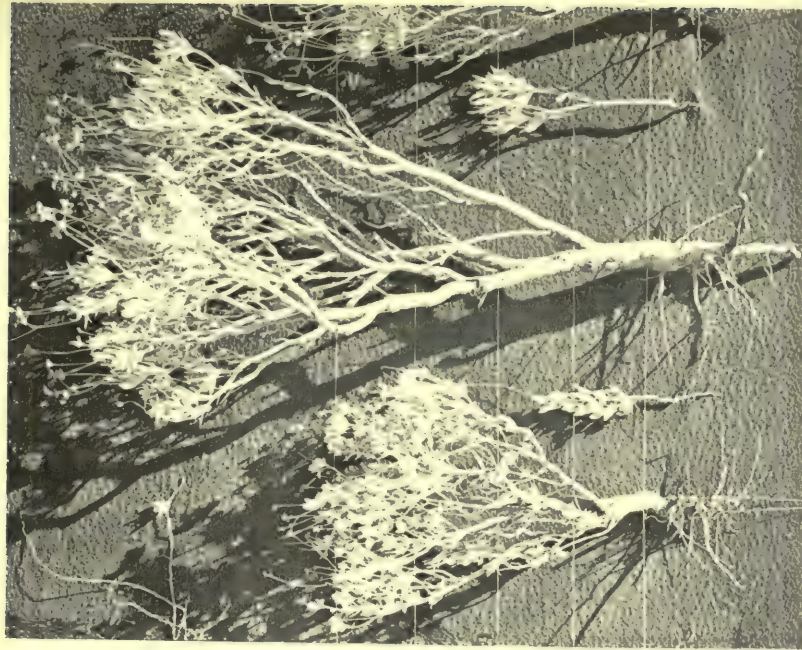
Finally, many guayule gatherers and others think to recognize different kinds as to color-characters, either of the bark or of the leaves. In Durango white guayule ("blanco") is distinguished from dark or "prieto," though no other characters could be pointed out to separate the two kinds. Indeed, when a branch was exposed to view in one position, so that the under surface of the twigs was seen, it was pronounced "prieto," and when the upper surface of the same branch was later shown it was called "blanco." This color difference, as between the upper and lower surfaces of the branches, is quite constant.

"Blanco" and "ceniso" or ashy guayule are maintained to be different also, though the same difficulty of seizing upon other than mere color differences obtains. So far as I could determine, "ceniso" guayule was shrub which had been exposed to severer drought, in consequence of shallower soil in exposed positions, as on benches, and in which the leaves had therefore dried to a dirty-yellowish color. Prolonged study might, however, discover that some of these differences are constant and racial, and the matter therefore deserves more consideration.

### SIZE.

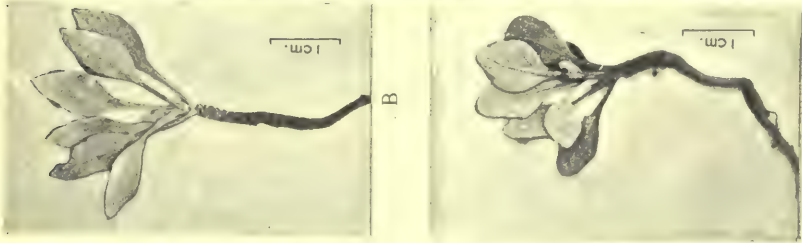
The question is often asked, especially by persons interested from the business point of view, as to the size which the guayule attains. It may at once be said that anything like the maximum size is a matter, or will be shortly, of academic rather than economic interest. Once the





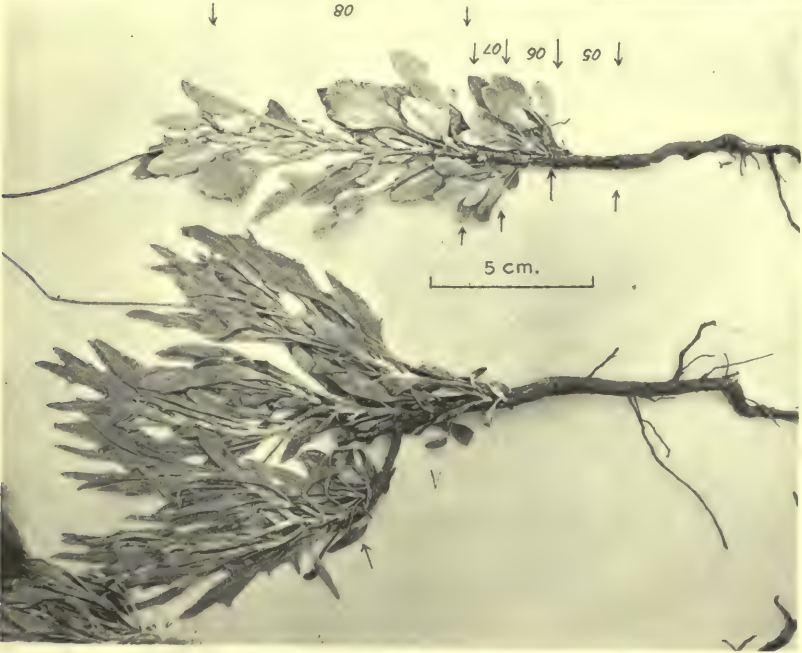
D

D. Seedlings and mature plants of these biotypes.



C

C. Seedlings of typical and atypical guayule.



A







A. An irrigated plant, from a small stock, at the height of flowering.  
B. "Embra" (on the left) and "Macho" (on the right) guayule.





virgin guayule has been removed, big plants will no more be seen. The largest plants which have been reported weighed in the neighborhood of 10 kilograms. Overseers of field experience insist that they have seen and weighed such. Endlich (1905) quotes Marse as having seen a plant weighing 6.5 kilos; but a plant weighing over 5 kilos is exceptional. Of three large plants which are illustrated in this paper, that in plate 12, fig. A, weighed 10.56 pounds (fresh weight), was 75 cm. tall, and 125 cm. wide. Plants over a meter in height are seldom met with, and are nearly always more or less stag-headed and moribund (plate 10). They have usually lost a good many limbs, and for many years have not been making any net gain in weight. Endlich places the average weight of virgin guayule at 500 or 600 grams. As will develop in the discussion in the following chapter, plants of this size, which would be 40 to 50 cm. or more tall, will in the future be considered large plants.

#### SURFACE CHARACTERS OF THE STEM AND METHOD OF DETERMINING AGE.

The importance and difficulty of determining accurately the age of a particular guayule plant has prompted careful study of the appearance of the surface of the stem at various ages (plate 14, fig. B). This appearance is due to (1) the primary superficial characters (epidermis, leaf-scars) and (2) the succeeding secondary cork. Secondary changes in the cork are produced by weathering. As marks also aiding in the determination of age may be mentioned the dead but persistent peduncles and the number of divarications of the stem, as related to the formation of inflorescences. Data relating to the rate of growth of seedlings, the marks of which are usually quite obliterated in plants taller than 10 or 15 cm., must also be considered.

#### FIELD PLANTS.

Let us suppose that we are examining a plant at the close of the growing season of, say, 1908. The characters seen in the accretions for the years mentioned will be as follows:

1908. Leaves still adherent. The epidermis is intact and densely clothed with appressed T-shaped hairs, producing the greenish-gray color uniform with the leaves. If the length of the year's growth is exceptional, say above 10 cm., the basal part may show slight longitudinal fissures. Diameter at base 3 mm. or less, rarely more.

1907. Epidermis still adherent, but more or less fissured, showing yellow cork. The hairs have been partially removed by attrition and withering, but most of them remain, preserving a gray color. Epidermis light brown. Leafless, but scars present. Often with short spurs, or undeveloped branches with each a few leaves. Diameter usually between 3 and 4 mm.

1906. Color gray, slightly slaty brownish, generally fissured, the fissures shallow, disclosing a gray-colored cork (weathered), with small areas of epidermis remaining between. Diameter about 5 mm.

1905. The growth for this and earlier years is dark gray, becoming darker with age. The fissures are shallow, becoming deep only with an age of over 10 years. The fissuring is deeper, and lenticels are more abun-

the period was at an end. This does not mean, however, that fresh flower-buds were not available and ready to develop, but that the water-supply was insufficient to support the heavy foliage and to enable the full development of the flowers as well.

The end of the flowering season is shown as much by the abortion of the immature capitula as by any other behavior. This is but the extreme expression of a very general phenomenon, that of the unequal development of the inflorescence in adjoining situations. When water is abundant the inflorescence is widely spreading, the result of the development of the pedicels (fig. 10), while where the water-supply is meager, but not insufficient for the development of the flowers, the pedicels may remain very short and thus produce a crowded mass of capitula. This condition is usually met with in the field (plate 2), and between this and complete abortion of the flowers every degree of failure to flower is seen, the result of reduced water-supply.

While the grand flowering-period falls normally in the summer, the exigencies of rainfall may so modify the rhythm of the plant that it will occur in, possibly, any month of the year. Under irrigation flowering starts in March,<sup>1</sup> and there is sustained a profusion of flowers through April (plate 14, fig. A) and May. It then dwindles, a second period of low maximum occurring in August, to be continued irregularly and with less perfectly developed flowers into November. In the field abundant flowers were observed in October in Durango (Hacienda de los Sombretillos) and in Sierra Ramirez, Zacatecas. Up to this time of the same year (1907) no flowers had been produced in the Sierra Mojada on the Hacienda Santa Inez, in Durango, where the guayule plants, forming an almost pure culture, were in a shriveled condition for lack of water.

Under favorable conditions the development of the inflorescence takes about two weeks. The flowers emit a delightful fragrance which attracts many small insects. Among these visitors mosquitoes were observed, extracting the nectar from the ray-flowers.

### THE PRODUCTION OF SEED.

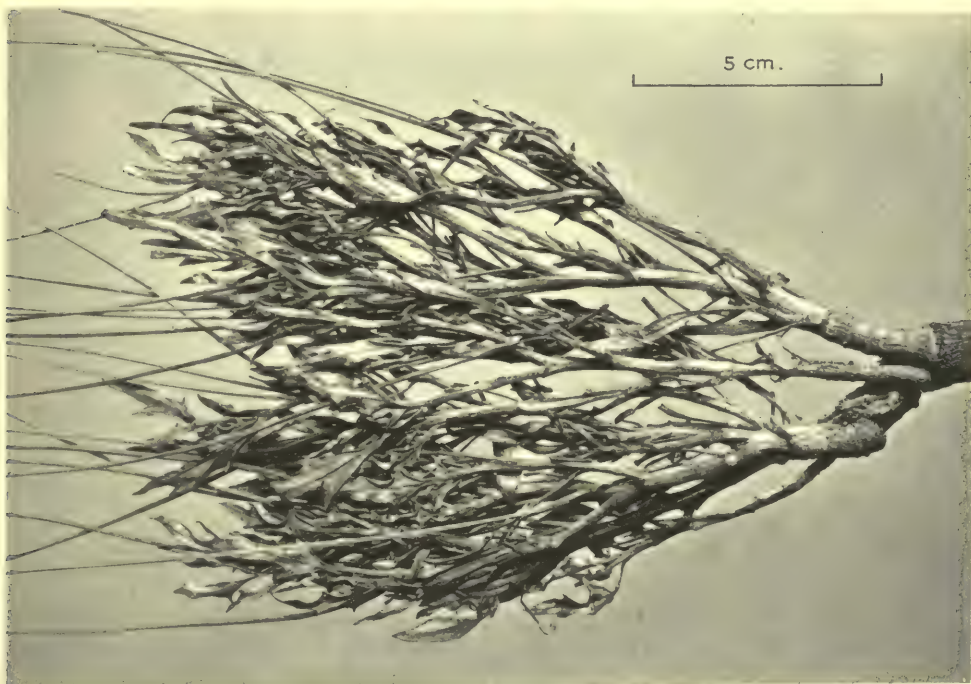
Though the maximum number of seeds which may be produced by each capitulum is only 5, the total number yielded by a moderate-sized plant may amount to many thousands. The percentage of viable seed, however, runs small. In a field-plant with well-developed heads less than 5 per cent of well-filled achenes were found. In other plants as high as 25 per cent were found filled. In irrigated plants the percentage rises considerably higher, namely, to about 35 per cent. When the achenes are fully ripe the bracts become brown in color and fall away from the pedicels quite easily. The collection of seed (Chapter IX), which must be done by hand if at all, should begin to give the best results at the close of the first period of flowering. Properly done, the flowers are stripped from the peduncle, which need not be removed from the plant. The nature of the "seed" has already been discussed.

<sup>1</sup> In 1909 flowering did not begin in these plants before the middle of April. Inquiry developed that they had not been irrigated freely, if at all, though of course the soil was much better supplied with moisture than that of the field.





B. Induced retoño on a lateral root. One season's growth.



A. Induced retoños on a tap root. One season's growth.





## CHAPTER IV.

### REPRODUCTION.

#### METHODS OF REPRODUCTION.

It is the purpose of the present chapter to compare the two methods of reproduction, sexual and vegetative, with reference to final efficiency in reproducing the species. It need scarcely be said that, in speaking of sexual reproduction, we are using the term to indicate the origin of the seed. It will be at once accepted that accurate knowledge of the topic here to be considered is of vital importance in deriving estimates of the rate at which guayule fields may be expected to produce a crop of that plant.

From what has been said in the foregoing chapter it will be seen that, taking different kinds of habitats into account, an average rate of reproduction will be maintained by means of the retoño and seed methods combined. The relative efficiency of the two methods depends upon widely different considerations, and these, as we shall now see, have relation to numbers of individuals, rate of growth, and the time of the year at which they begin this growth.

#### RETOÑOS, NORMAL AND INDUCED.

We may speak of two kinds of retoños, normal and induced. By normal we mean those which arise spontaneously upon the lateral, superficially placed, horizontal roots, remaining for some time attached to the plants from which they spring (plate 9). Induced retoños (plate 15) will then be those which arise as the result of mutilation, that is, from roots, primary or of a higher order, after the plant has been cut away. This is done on a number of haciendas in the harvesting of the shrub, whereas the plants used to be, and by many still are, pulled up by the roots. This pulling results, of course, in breaking away many of the roots, but the chief portion of the tap-root is removed, as also are considerable lengths of the other roots. As we shall see, the difference in effect upon reproduction is merely quantitative, as in both cases retoños may arise, but in very different numbers. In order to test this with as great accuracy as possible, quadrats of 100 square meters were cleared of the guayule both by the cutting and pulling methods, and the results were noted. These, for the quadrats observed, afford accurate data, which must be understood as of indicative value only. It may well be believed that different meteorological conditions would have modified the results very considerably. Thus, if the experiments had been started just at the beginning of the summer rainy season more hopeful results might have been had, but we shall see that cutting at this time is for other reasons an unfortunate practice, and the evil resulting would offset the value of the data thus obtained. It is well, therefore, for economic reasons, that the data collated shall be well within bounds. In addition to experimentally obtained data, others derived from observation are given, and have already been discussed in part in Chapter III.

## GENERAL OBSERVATIONS.

It is generally believed that, after a field has been harvested of its guayule, it will reproduce itself in a short period of years, the length of which is a matter of opinion. Estimates on this point vary from 5 to 10 years.<sup>1</sup> As, however, this difference in length of reproductive period, which we may call the period of rotation, involves so large an error in returns on investment, an effort to get at the facts is eminently justified. From the botanical point of view, the rate of reproduction and of growth of desert plants has been so little studied that data bearing on these questions are of great importance, especially as the eye of civilization is being turned on the desert as a field in which must be developed the natural resources peculiar to it.

## NORMAL RETOÑOS.

The number of plants which arise as retoños within a given area is, with probably few exceptions, small.

TABLE 20.—*Comparative numbers of seedlings and retoños in given areas.*

Locality.		Number of small plants (below 8 oz.).	
Station.	Quadrat.	Seedlings.	Retoños.
8.....	2	36	4
8.....	1	14	2
9.....	1	86	4
9.....	2	5	1
10.....	..	90	8
11.....	..	232	0
12.....	..	200	0

These numbers are accurate as far as they go, but they do not tell what proportion of all the plants of the quadrats mentioned arose as retoños. In the vicinity of Station 2 plants of this sort could easily be found, and all but one of those in plate 9, fig. B, were obtained in a restricted area nearby, especially on the steeper slopes. But for all this, the total numbers of plants which have arisen as seedlings, taking all the areas into consideration, must far outnumber retoño plants. On irrigated plants 2 years old, some 150 in number, not a single retoño was observed, a fact which may perhaps be correlated with the weaker development of shallow lateral roots in such plants. Only one instance (plate 46, fig. B) of a retoño starting under irrigation has come to my notice. Numerous adventitious buds were distributed on the mother-root, evidently having started after the plant was pollarded. This was done, not at the time of transplanting, but some time later, when it was discovered that the plant was not responding. The importance of normal retoños, therefore, is not to be seen in the numbers but in other qualities (Chapter III).

<sup>1</sup> At the present writing we read in a recent number of the *India Rubber World* (March 1909), that a new crop of guayule may be expected in "a few years." We may suppose that heavily interested investors have obtained accurate information upon which they base their operations, but none, so far as we are aware, have been given publicity.



Normal retoños usually begin their growth with the oncoming of rain, especially in spring and early summer. In this regard they act merely as expressions of growth and have no special peculiarities. Starting as they do from the shallow-lying roots, they make an etiolated growth of a few centimeters before emerging from the soil. Their rate of growth depends upon the size of the root from which they spring and the numbers arising at one point. If the root is slender growth is relatively slow, and subsequently depends on the rate of secondary growth of its distal portion; if large, the retoño grows rapidly and may in a month or two attain a height of 10 or 15 cm., a rate scarcely to be met with in the case of seedlings. A notion of the rate of growth may be had from the following table of measurements, based upon the specimens in plate 9, fig. B, the numbers referring to those similarly numbered in the figure.

TABLE 21.—*Size, age and weight of plants which arose as retoños (referring to plants in plate 9, fig. B.)*

Plant.	No. of stems at base.	Height of stem.	Diameter of stems.	Weight, fresh.		Age.	
				lbs.	oz.	yrs.	mos.
1 ..	4	43	$\begin{Bmatrix} 23 \\ 21 \\ 24 \\ 16 \end{Bmatrix}$	1 <sup>2</sup>	8	8 to 9	
2 ..	1	28	20		8	8	
3 ..	7	20	4.5 to 8		3.5	4	
4 ..	5	16	5 to 8.5		6	4	
5 ..	3	14	5 to 8		2.875	3	
6 ..	3	20	7.5 to 10		3.25	3	
7 ..	1	18	17.3		3	4	
8 ..	4	14	4		20.56	2	
9 ..	2	13	3		....	2	
<sup>3</sup> 10 ..	4	10	1.5 to 2.5		....		4
<sup>4</sup> 11 ..	3	6	2.5		....		2 to 3

<sup>1</sup> Dry weight 1 lb. 5 oz.

<sup>2</sup> Dry weight.

<sup>3</sup> Induced by cutting away the plant, January 1908.

<sup>4</sup> Grew in season of 1908.

It is at once apparent that, as compared with the rate of growth of seedlings, that of retoños is much more rapid. It takes at least 15 years to produce a plant of 2 pounds weight from the seed. Plant No. 1, in the above table, made its weight in certainly not more than 9 years, possibly in 8. This is brought about by (1) the more numerous stems arising from the base and (2) the more rapid elongation of the stems, due to the advantage had in the already established root-system. Table 20 affords comparative data as between seedlings and retoños. Incidental advantages accruing from this purely vegetative method of reproduction are (1) relative certainty of success because of the previous establishment of the parent plant, with relative independence of an initial good season in order to start, and (2) the rapidity with which the plants arrive at a condition to flower abundantly; e.g., plant No. 11, a few months old, produced fully 100 seeds. These, in a desert especially, are no mean advantages. Thus, they would enable a single guayule plant to compete with such a plant as the lechuguilla, assuming that it had so fully occupied the ground that

seeds could not get started, by maintaining a foothold till the dying off of lechuguilla plants, say as the result of flowering, allowed seedlings once more to take hold.

#### INDUCED RETOÑOS.

In order to determine the number of retoños formed after pulling up (usually called "cortando") and after cutting away guayule plants, the following experiments were made:

*Experiment 115.*—Station 2, quadrat 4. Jan. 6, 1908. 250 plants, all under 40 cm. in height, were pulled up by hand, leaving in the ground only such roots as were broken off by chance. Feb. 18, no growth; Mar. 29, no growth; Apr. 28, 5 roots produced retoños; July 28, 9 clumps of shoots from as many roots started. Sept. 12, none additional. Apr. 3, 1909, 6 additional roots had started.

The following measurements were made of dried material collected on April 3, 1909:

TABLE 22.—Station 2, quadrat 4. Induced retoños.

No. of stems on each root.	Height of stem.	Diameter of stem at base.	No. of stems on each root.	Height of stem.	Diameter of stem at base.
	cm.	mm.		cm.	mm.
2	13.5	7, 8	1	6	3
2	13	3, 10	5	4 to 7	3 to 4
2	15	7, 9	6	3 to 4.5	2 to 3
1	9	10	3	4 to 8	2 to 4
1	10.5	8	3	4.5 to 7	1 to 4
6	6	3 to 4	25	1 to 7	1 to 4
1	8	5	2	9, 10	4, 4.5
10	2 to 7	2 to 4			

The average amount of growth in stem-length was 8 cm.; in diameter 4.4 mm. All of the new growths produced flowers, and were in normal condition when examined at the close of a long drought period. One of them is shown in plate 15, fig. A.

*Experiment 114.*—Station 2, quadrat 3, Jan. 6, 1908. Of 338 plants, all but 88 small ones (*i.e.*, 250 plants) were cut off with a "talacho" from 1 to 5 cm. below the surface of the ground. No growth till after Mar. 29. Apr. 28, 1908, 40 clumps of new shoots well started, each clump of 2 to 6 shoots. Stems 4 to 6 cm. long, with leaves of the same length. The severed roots died back about 2 cm. before the new shoots started. Depth of soil at which the shoots started, 2.4 cm. July 28, 59 clumps of new shoots. Sept. 12, none additional. Length of longest stems, 10 cm. On Apr. 3, 1909, 6 clumps were removed and measured, the data from which are given in table 23.

TABLE 23.—Station 2, quadrat 3. Induced retoños.

No. of stems in clump.	Length.	Diameter.	No. of stems in clump.	Length.	Diameter.
	cm.	mm.		cm.	mm.
2	12	5	4	6	1 to 5
12	7	1 to 4	1	6	13.5
2	9	1, 4	1	10	8
Ave.	8.3	5	Ave.	8.3	5

<sup>1</sup>From a tap-root only 4.5 mm. in diameter.

Close by this quadrat a retoño (plate 15, fig. B) was collected, which had sprung from a lateral root 5 mm. in diameter. The chief shoot had 10 branches. Total height, 8.5 cm.; diameter at base, 5 mm. Number of inflorescences 8, producing 80 to 120 seeds.

Station 2, quadrats 5 and 6. Apr. 3, 1909. The following samples were taken at random, supplying the attached data for growth in 1908:

From a broken-off tap-root 7 mm. in diameter, 2 new shoots, 12.5 and 13 cm. long by 6.5 and 7 mm. in diameter, respectively.

From a broken-off tap-root 6 mm. in diameter, two new shoots 6.5 and 3 cm. long by 3.5 and 1 mm. in diameter, respectively.

From a lateral root, a clump of 5 stems, each 2 cm. long.

*Experiment 110.*—Station 3 (one quadrat). Dec. 31, 1907. 30 plants, 30 to 60 cm. tall, cut off with a talacho. No growth observed on May 1 following, till which date there was no rain. July 16, 3 roots had started. A number of roots, including the 3 which had started, were taken up for examination and the data tabulated as follows:

TABLE 24.—Station 3 (*exp. 110*).

No.	Order.	Position.	Died back.	Diameter of root where cut.
1	Secondary.....	Nearly horizontal....	cm. 25	mm. 10.5
2	....Do.....	....Do.....	13	8.0
3	....Do.....	....Do.....	7.5	4.0
4	....Do.....	....Do.....	13	5.5
5	Primary.....	Vertical.....	12	11.0
6	....Do.....	....Do.....	3	17.0
7	Secondary <sup>1</sup> .....	Horizontal.....	20.....	5.0
8	....Do.....	45°.....	2.6; merely started	4.0
9	....Do.....	45°.....	13; started; shoot 2.5 mm. long.	6.5
10	....Do.....	Horizontal.....	<sup>2</sup> 10.5.....	....

<sup>1</sup>Arising from No. 6 at 2 cm. from the top, where cut.

<sup>2</sup>Started (in 1907?) shoot 7.5 cm. long.

*Experiment 121.*—Station 4, quadrat 1. 50 plants in all. These were cut away as in the other experiments, Jan. 14, 1908. May 6, no growth whatever apparent. A rain-gage was placed at this station on Jan. 14. May 6: rainfall registered to this date, 1.52 cm.

Apr. 5, 1909, 6 clumps of retoños. This appearance of new growth followed on further rainfall, as evidenced by the rain-gage of Station 5, a short distance away.

*Experiment 125.*—Station 5, quadrat 1. Jan. 15, 1908. 275 plants cut off below level of ground with a talacho. May 6, 30 roots have started, sending up 1 to 5 shoots each, but smaller than those at Station 2. Between Jan. 15 and May 6, rainfall 353 mm.

Apr. 5, 1909. 43 clumps of retoños. The increase in numbers was the result of the additional rainfall, as indicated by the rain-gage, which was still in position, though standing somewhat obliquely. Evidently some of the water had been lost, as the oil had disappeared. The amount remaining, 700 c.c., indicated a total precipitation of at least 850 mm. Length of new stems, 7 to 15 cm., with diameter of 2 to 9 mm.

*Experiment 131.*—Station 3. Dec. 31, 1907. 100 square meters. 30 plants cut off at surface of ground. No new growths till after May 1. July 15, one retoño. Apr. 2, 1909, two retoños in all.



The percentages of removed plants represented by new shoots in all the above experiments are as follows:

	<i>Per cent.</i>		<i>Per cent.</i>
Experiment 115 (pulling).....	6	Experiment 110 (cutting).....	10
Experiment 111 (cutting).....	6	Experiment 121 (cutting).....	12
Experiment 114 (cutting)..... <sup>1</sup>	23	Experiment 125 (cutting).....	15

From the above data the following conclusions may be drawn:

Retoños are formed much more easily from the stock left after cutting at or near the level of the ground. The probability that the plants removed will be represented by new growths after cutting is much greater when a portion of the stem at the top of the tap-root is left. This is due, of course, to the presence of numerous dormant buds.

The promptness with which retoños start after cutting away the plants depends, in the absence of sufficient soil-moisture, upon the rainfall. It is worthy of note (1) that these retoños may start slowly before the advent of rain, and (2) that the roots may die back at least 13 cm. before starting. Root No. 1, experiment 110, had died back 25 cm. during six and a half months, that is, at the rate of about 4 cm. per month, and it finally failed to start. It was a very dry period, and this long tenacity of life illustrates in a striking way the physiological resistance of these roots in desert conditions.

While this degree of hardiness would serve very effectively to preserve the species under unfavorable circumstances, it is evident from our figures that the number of new plants produced is not as great as is generally supposed. The best result obtained (exp. 114) indicates that under the conditions surrounding this experiment scarcely more than 25 per cent of the original stand may be expected. It is a matter for satisfaction, however, that even under the most drastic treatment a field of guayule may be expected to reestablish itself in the course of time, since the new growths will in a short time be able to produce seed and these will contribute to the repopulation of the area.

In April 1909, two areas were visited from which the guayule had been removed by pulling up the shrub. It appeared that only the larger plants had been removed, and that both places still contained the natural growth of smaller plants. The point of interest in this connection is that in one of the areas, the Lomerio de Zorrillos, it was very easy to find broken-off roots which had started to grow again, and retoños of various sizes up to 8 cm. were found. In the other area, in the Sierra de Ramirez, the ground was very hard and the peons found difficulty in pulling the plants out. Instead, they had twisted them off just above the surface, and from the butts remaining, with very few exceptions, new shoots had grown during the season of 1908, these measuring from 3 to 8 cm. in height. This parallels the behavior of plants cut off at some distance above the surface of the ground.

*Experiment 60.*—Station 2, quadrat 1. 25 square meters. Nov. 5, 1907. 140 plants cut off at a height of 8 to 10 cm. above the surface of ground.

<sup>1</sup> The total number was not determined in April 1909, but would doubtless have indicated a larger percentage.

- Jan. 6, 1908. Many buds 2 mm. long.  
 Feb. 18. All but 5 plants budded. Longest leaves, 25 mm.  
 Mar. 29. Little change. Longest leaves, 30 mm.  
 July 28. 5 plants dead. Longest stems of new shoots, 7 cm.  
 Sept. 12. 12 dead altogether. New shoots 10 to 15 cm. long. Plenty of flowers. Some plants have the appearance of witches' broom.  
 Apr. 3, 1909. 13 dead. Maximum stem-growth, 20 cm.; minimum, 3 to 5 cm. New shoots in several cases killed by drought (plate 16, figs. A to C).  
*Experiment 56.*—Station 1, quadrat 2 (25 square meters). All plants cut off as in experiment 60, Nov. 5, 1907.  
 Jan. 3, 1908. No growth.  
 May 29. New stems (upwards of 15 mm. long, 4 mm. diameter) on the majority of cut stems.  
 Apr. 3, 1909. Maximum growth, 10 cm. stem-length.  
*Experiment 126.*—Station 5, quadrat 2. Jan. 15, 1908. All plants cut at 15 cm. above ground.  
 May 6. Nearly all well budded.  
 Apr. 5, 1909. New shoots 10 to 15 mm. long; flowered well in 1908.

From the rainfall data it appears conclusive that the best time to cut guayule, with reference to reproduction by retoños, is just before and during the rainy season. As we shall see, however (Chapter V), this is the period of active growth, and the rate at which the accumulation of rubber takes place is such as to indicate that the practice of removing guayule at this time is not advisable. Therefore, other considerations aside (such as competition with other plants), the removal of guayule even during the most trying seasons will not exterminate the plant, except on restricted areas which may be rehabilitated by spreading through seed. It is scarcely to be doubted that even in the quadrat of experiment 121 a few retoños made their appearance after the last date of observation, which, unavoidably, was before the summer rains.<sup>1</sup> Furthermore, we are able to say from observation that the conditions at this station were more rigorous than at Station 2, where an earlier start was made by the retoños.

The rate of growth of induced retoños will be seen to exceed the initial growth of seedlings. The stem-growth for the growing-season of 1908, as shown by observations taken on the above experiments in April 1909, was upwards of 15 cm., the average amount of growth falling somewhere near to 8 cm. The retoño in plate 9, fig. B, plant No. 10, made a stem-length of 10 cm. in about three months, and would probably have made more growth had it been allowed to remain.

As between the pulling and cutting methods of gathering guayule, there can be no two ideas as to the relative effect upon the rate of reproduction by means of retoños. In adjoining quadrats (experiments 114 and 115), in which it so happened that the same number of plants was removed, in the one by cutting and in the other by pulling, the clumps of retoños were as 59 to 15. This is explained by the fact that the roots left in the ground when the shrub is pulled up are not only fewer in num-

<sup>1</sup> After this was written this quadrat was visited on April 5, 1909, and it is of interest to note that the belief expressed was substantiated. See experiment 121, above, on page 65.

ber but smaller than those left when the shrub is cut. The larger break off further in the ground and are therefore less favorably placed for starting afresh. The disadvantage of the cutting method in the eyes of those who are in pursuit of the greatest possible initial return is that less tonnage per acre is obtained, a loss, however, which would be made good many times in new plants if the roots were properly cut and allowed to remain.

#### SEED.

##### VIABILITY.

The seeds of guayule appear to have a fairly long period of vitality, a conclusion, however, which is inferential and has not been demonstrated by direct experiment. The view is based on the following experiment (exp. 78): On November 23, 1907, a lot of trays (such as are shown in plate 45) were filled with paper tubes of 1 square inch transverse section. The trays were then filled with soil made up of half and half garden soil and old dry manure from a horse corral. In the top of each tube were sown 20 to 30 seeds. The trays were watered abundantly by subirrigation, it being the purpose to try the method of using the trays with paper tubes for wholesale germination. So far as this was concerned, the experiment was a failure, but it served to contribute to our knowledge of seed vitality. The very dry season made it very difficult to keep the surface soil moist, and as a result of alternate drying and wetting the upper part of the soil became caked and there was considerable efflorescence of salts. The soil below became soggy and sour, and fungi permeated the soil and the paper of the tubes. Very few seeds germinated, not more than one or two in each tray, partly, as was later determined, because of the character of the soil, and partly because of the prevailing low temperatures. The trays lay thus, occasionally wet by showers, till the following July, when a large number of seeds started to germinate. In one tray 138 tubes had seedlings, from one to eight in each. By July 25 the seedlings had developed two foliage leaves, and by August 28 a stem-growth of 5 cm. was not exceptional, with leaves 5 cm. long. Some plants had at this date as many as seven foliage leaves. Thus it will be seen that the seeds which germinated did so after six months' exposure to conditions about as bad as could be imagined, being alternately wet and dry, in a sour soil, and open to the attacks of fungi. The germination in trays favorably placed with respect to shade was upwards of 13 per cent of viable seed, as nearly as may be calculated.<sup>1</sup> It may therefore be concluded that the seed of guayule, being neither very short-lived nor very sensitive to untoward conditions, is, from a biological point of view, quite efficient for the preservation of the species.<sup>2</sup>

It is, in the nature of the case, well-nigh impossible to determine the percentage of germination of nature-strewn seed, but one successful experiment affords us exact data (experiment 192). On May 30, after a

<sup>1</sup> Critical germination tests to determine the viability of seed have been made by Kirkwood (1910a), who finds the germinations to scarcely exceed 14 per cent, and that after eight months there is a marked drop in viability.

<sup>2</sup> Ready germination from seed collected during the summer of 1908 was obtained in July 1909, at Auburn, Ala.





C



A



B



D



E

A--C. New growths after pollarding. A, February 18, 1908;  
 B, March 29, 1908; C, April 5, 1909.  
 D. Seedlings in limestone soil; E, in "garden" soil.





A



B

A. Minimum, average, and maximum seedlings. (Station 2, quadrat 4.)  
B. Irrigated plant, two years old, from a stock. April 1909. Cedros.





rain of 16.8 mm. during the preceding night, 4 ounces of seed (including chaff) were sown at Station 7, in 5 rows, each a meter long. The ground was previously cleared of all plants and thus loosened, and, the seed having been left uncovered, the seedlings were exposed to full insolation. On September 9 following, 119 seedlings were counted.<sup>1</sup> These compared favorably in appearance and size with other seedlings found growing spontaneously in the surrounding area. The seed was sown more thickly than would occur in nature, and the number of seedlings was also much greater, and far too great for their normal development.<sup>2</sup>

Comparison of these results with those obtained by observation of germination in irrigated ground affords considerable interest. About 150 plants, placed in a small patch of ground by Mr. C. T. Andrews in the spring of 1907, flowered freely during that and the following year. A very large number of seeds must have been disseminated, notwithstanding a good deal had been gathered, of which fully 30 per cent were viable. During the summer of 1908, at the time (June) when seed was germinating in the surrounding region under natural conditions, some seedlings were observed. About 50 were counted, but in the whole area (0.1 acre) there could hardly have been more than a few hundred at the outside. Nor did they grow as well as field seedlings, perhaps because of the rapid drying of the superficial layers of soil. The percentage of germination here must therefore have been exceedingly small, and much less than that which occurred in experiment 192 above described, and also than that which takes place in nature, if we may judge by the numbers of seedlings actually found in the field in the summer of 1908. The following observations are pertinent here:

- (1) *Station 3*. June 1908. In areas of 1 square meter, representative counts of 8 and 14. April 1909, 23 living seedlings of 1908 were found on the whole quadrat (100 square meters).
- (2) The region about *Stations 7 and 8*. On June 24 a large number of seedlings was seen.
- (3) *Station 2, quadrats 5 and 6*. Sept. 12. Four seedlings 10 cm. apart. Nearby 6 seedlings 10 cm. apart. Several counts showed about 20 plantlets per square meter. None on previous visit to this station, July 28.
- (4) In 1 square foot on the same area, 6 well-grown seedlings. Sept. 12, 1908.
- (5) In a wire-fenced quadrat which was cleared of all plants (other than guayule) by Mr. C. T. Andrews early in 1907, 5 miles north of Cedros in an open plain, leaving one tall guayule plant in the middle, no seedlings appeared till after June. In September 29 seedlings were found within 6 feet of the plant, chiefly in one direction. One mariola seedling was found.
- (6) *Station 8, quadrat 1* (100 square meters). 24 seedlings, Sept. 1908.
- (7) In 4 square feet, on a loma north of Cedros, near Station 8, Aug. 8, 31 seedlings, all of 1908 except one of 1907. This number included one of *Parthenium hysterophorus*.

<sup>1</sup> The largest of these had a stem (epicotyl) 1 cm. long, with leaves 4.7 cm. long by 1.5 cm. broad.

<sup>2</sup> In April 1909 it was found that all the seedlings had been destroyed by goats.

- (8) Near this place 22 seedlings were collected from two areas, each of 12 square inches; 1 of 1906, 8 of 1907, and 13 of 1908.
- (9) Station 2, quadrat 4. April 1909. 281 living seedlings, all of which germinated during the growing-season of 1908, were collected on 100 square meters (plate 17, fig. A).
- (10) Endlich reports finding "as many as 50 young plants around full-grown trees" (335, 1905, Eng. tr.). Such a large number is not common, but it is not unusual to find 25 seedlings with two foliage leaves about the base of a single plant.

From such observations it is clear that in particular areas one may find by chance many more seedlings than could by any fortune develop into mature plants. Other areas, however, are quite bare of them. Again, many seedlings which get started die in the course of time, and there can be no doubt that the percentage of deaths is great. Counting seedlings, therefore, is not a dependable method of determining the rate of repopulation. For this purpose it is necessary to make a census of sample quadrats, making as careful estimates as possible of the sizes and ages of the plants. The data in tables 4 to 13 afford such a census. They are summarized in table 25 and are further displayed graphically in fig. 12.

TABLE 25.—Classification of guayule plants from seed according to weight on various quadrats indicated.

Quadrat.	4 lbs. or more.	3 lbs. or more.	2 lbs. or more.	1 lb. or more.	$\frac{1}{2}$ lb. or more.	Less than $\frac{1}{2}$ lb.
Table 4.....	0	0	0	10	100	585
6.....	0	7	13	15	11	26
7.....	7	5	13	40	4	10
8.....	0	2	12	20	9	86
19.....	0	0	0(?)	0(?)	250(?)	755
10.....	2	3	5	4	4	6
11.....	0	0	1	28	59	90
12.....	0	0	1	23	23	232
13.....	0	1	12	45	53	166

<sup>1</sup> It is to be recalled that the larger plants had previously been removed from this quadrat. The estimate marked doubtful is based on the figures of adjoining quadrats, and can only be approximate.

It is clear that the ratios between small and large plants, as shown in table 25, indicate very different degrees of efficacy in reproduction commencing from the seed. This method is the best available in the absence of actual counts of seedlings year by year, obviously not practicable. A few such counts, for future comparison, are given in table 26.

TABLE 26.

	Seedlings of 1908.	When counted.
Station 8, quadrat 1.....	24	1908
Station 3, quadrat 1.....	23	Apr. 2, 1909
Station 2, quadrat 4.....	281	Apr. 3, 1909

These few data, the difficulty of obtaining which, on account of various circumstances, was very great, have only suggestive significance. It is



obvious that in the last station reproduction by seedlings is relatively very good, especially as the counts were made at the close of a long drought. A condition such as this might, in the light of table 25, be expected to lead to a good stand of guayule. From a consideration of the curves based upon table 25, some further points of interest are discovered. There is a large falling off in numbers of plants between the average weight of about 4 and 12 ounces. This, as seen in the curves on pages 87 and 88, is the period, approximately, of maximum rate of growth, viz, between 8 to 10 and 13 to 15 years of age, during which time there is a loss of total weight of about one-fourth to one-third, as nearly as we may calculate. From the nature of the conditions, many of which are undeterminable, such calculations can be only loosely approximate, but it can hardly be doubted that, if the rate of reproduction by seed from plants, say from 6 to 8 ounces in weight, can be depended upon quantitatively as

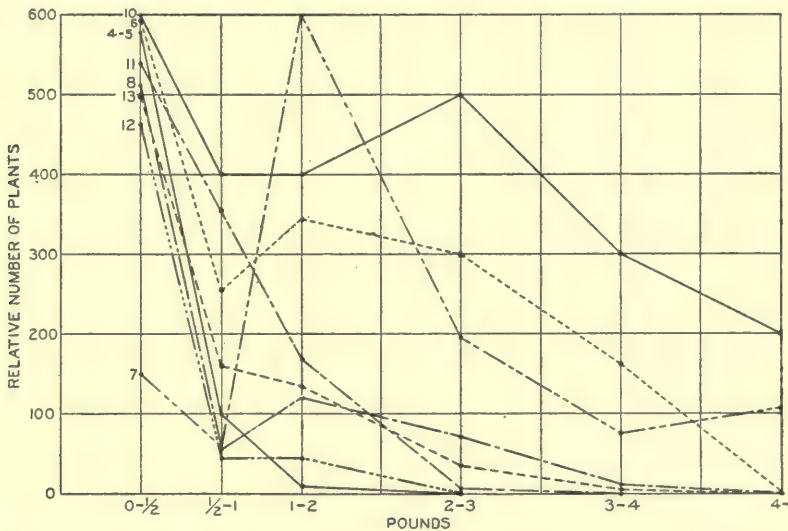


FIG. 12.—The relative numbers of various-sized plants on different quadrats. The numbers at the ends of curves refer to the tables corresponding.

indicated in the table under consideration, it is an economic loss to allow plants larger than these to remain. From this point of view alone it may not pay to allow the plants to remain after the age indicated by the weight of 6 to 8 ounces has been attained, as the numbers which die off are great enough to cause a considerable falling off of total weight.

The data show also that the initial monetary return from a harvesting of guayule may be as great or greater from a stand of a few large individuals, but the areas with large numbers of smaller plants give promise of future returns.

An important desideratum is to determine how to improve these conditions. Here, let us say, is a good field of guayule, as regards first returns. The bulk of the weight is in large plants, and the small ones are too few for a ready reseeding of the area after depletion. It is hardly too much to say that vast areas are in this condition. What may be

done to increase their productivity is still a question for experimental determination, but seeding in favorable years by means of seed from densely grown areas would be distinctly beneficial. The importance of seed is so great that in the harvesting of shrub the practice of leaving large plants for the purpose of producing seed should in all circumstances be initiated. As a practical question of economics, the difficulties of time and distance in the desert are so great, not to mention those arising in connection with climatic irregularities, that any attempts to better conditions over wide areas are fraught with expense which may not be considered as warranted by those interested.

#### COMPARATIVE ABILITY TO GERMINATE IN THE FIELD.

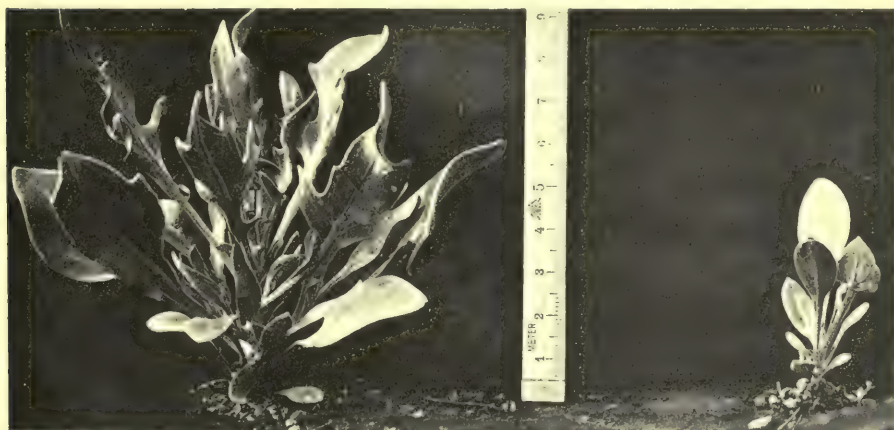
The ability to germinate promptly, to attain a condition of physiological resistance, is of prime importance to desert plants, and very much more important to them than to plants which are more favorably placed with reference to water-supply (Ganong, 1907; Lloyd, 1909a). So far as the question of germination is concerned the evidence is not forthcoming that desert plants exhibit more indifference to initial water-supply than others (Livingston, 1906). For the rest, as for further elucidation of this problem, much comparative study is necessary. There seems to be little doubt, however, that the rate at which physiological resistance is acquired and the amount of this resistance are very different in different plants. For example, the seedlings of many succulents soon acquire the characters of the parents, the cacti (Ganong, 1898) being notable examples of this. This must be of no small weight as a factor in enabling young plants to withstand the rigors of drought, though this very circumstance in the cacti opens them to the attacks of animals (MacDougal, 1910), so that millions of seedlings are eaten, affording both food and water to desert animals.

As has been shown, and as will be further developed in the following chapter, the guayule seedling offers no exception to the rule that desert plants need an abundance of water during the period of germination. Observation in the field indicates further that marked readiness in germination is not in any way indicative of adaptation to desert conditions. A field test of the germinating ability of guayule in comparison with that of *alfilaria* (Station 7, May 30, 1908, exp. 139) showed that about 3 per cent of the seed of the latter germinated, while about 0.2 or 0.3 per cent of guayule succeeded in getting a foothold in the same place under the same conditions. These figures are probably too low for both plants, inasmuch as ants were observed carrying off seed on each occasion that the station was visited. This test, however, may indicate the direction in which research may contribute toward the explanation of the success which the *alfilaria* has had in invading desert territory.

A further observation was made at Camacho, on the Mexican Central Railway, on the Hacienda de Cedros, a point for the shipment of guayule, where a stack-ground had been kept supplied with shrub from the neighboring region. It is customary to bring in the shrub in loose bundles on the backs of burros or in carts of various sizes and kinds to these shipping-points, there to be made up into bales for handling on the railroad.



A

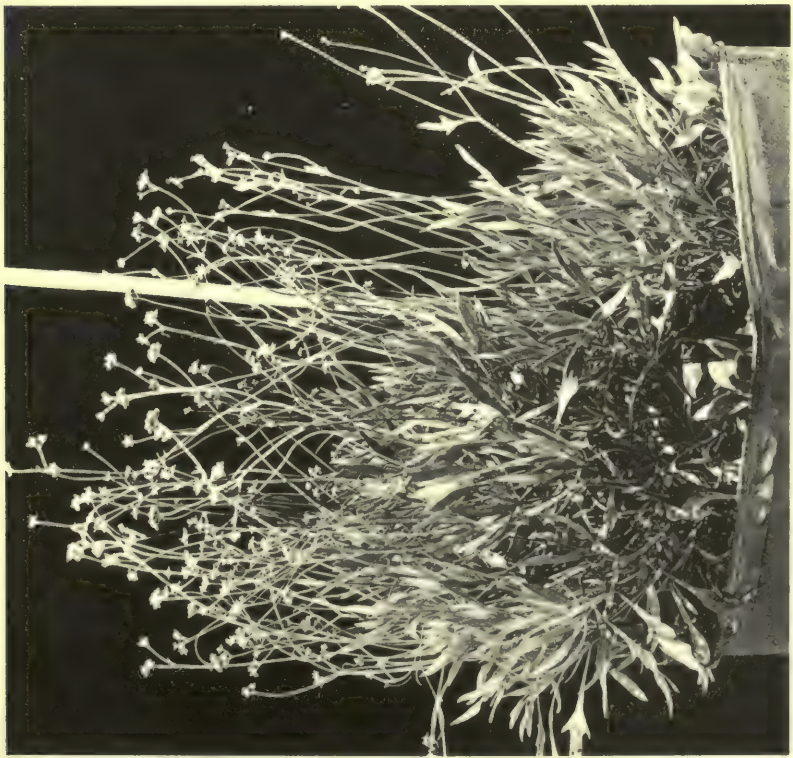


B

Seedlings growing in different soils: A, May 25, 1908; B, April 13, 1908.







A

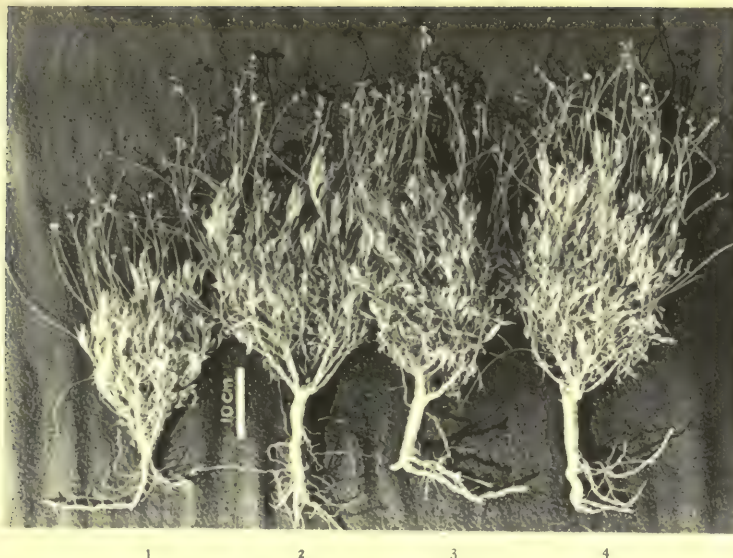


B

Seedlings growing in different soils: A, June 8, 1908; B, May 5, 1908.







A



B

A. (1) Root-cutting; (2 to 4) Sectional root-stem cuttings (Exp. 146).  
B. Seedlings grown in different soils, August 1908.



Countless numbers of seeds are therefore strewn upon the ground, and indeed the new plants of guayule which spring up on these stack-grounds sometimes afford valuable data on the rate of growth, although deceptive notions as to the numbers of plants which may be expected are sometimes acquired. The conditions of a stack-ground are, at Camacho at least, a rather severe test, as it lies out in the open, dry plain, exposed to full sunlight. At the same time, the surface of the soil is mulched by the débris of broken-off guayule twigs, and thus the conditions are ameliorated. Shipments, which had been made for a year or longer, ceased in the fall of 1907, and the spot was under occasional observation for some time before and from that time on, till the following September. Although it is known that much guayule was brought in in flowering condition and that seed must have been dropped in large quantities, the conditions for germination, especially the meager rainfall, were not favorable for guayule, though the seeds of the plants in the following list were found in all conditions of development in June and July of 1908:<sup>1</sup>

*Helianthus* sp. 15 to 18 inches tall and many in flower.

*Amaranthus*, 2 species. Plants 3 inches tall.

*Cassia* ("coco"). Many mature plants in flower.

*Prosopis* seedlings with the plumule well developed.

*Euphorbia* of 2 species. Mats 10 inches in diameter.

*Solanum* sp.

A cucurbitaceous vine.

*Chenopodium*, a species with broad deltoid leaves.

Grasses of 4 species.

*Spheralcea*, mature plants.

In addition to these seedlings, the roots of *Prosopis* and *Covillea*, which had been cut off in preparing the ground for stacking, had sent up shoots from 10 to 20 inches in length. That not a single guayule plant sprang up is at first surprising, not to say disconcerting, but in the light of experimental evidence it becomes clear that the guayule germinates only under highly favorable conditions. For some time it has a low degree of resistance, and is in point of fact of distinctly mesophytic character. It is only when due regard to this is had that the maximum rate of germination may be expected under cultural conditions.

#### HABITATS OF SEEDLINGS.

The particular preference of the guayule for certain germination habitats is of importance in its bearing on the effect of clearing land of other plants. It has been repeatedly observed by the investigators at the Desert Botanical Laboratory, and by myself in Zacatecas, that there are usually to be found many more plants of smaller size growing in the partial shade of shrubs than elsewhere, and it is to the protective effect of this shade that the many curious juxtapositions of perennial plants may be referred. An example of this is the frequently seen saguaro (*Carnegeia gigantea*), standing in a position indicating that it germinated in the shade of a palo verde (*Parkinsonia microphylla*) or some other shrubby species.

As regards the guayule, Endlich (1905) speaks of "the large numbers of young plants sometimes found surrounding the older trees \* \* \* in the

<sup>1</sup> Every annual had disappeared by April 1909.



territory around Jimulco, for instance, as many as 50 young plants have been found around full-grown trees." But, on the other hand, speaking of the occurrence of young plants in supposedly very unfavorable spots, Endlich explains this by saying that "it is likely that they have been developed from such seeds as were either stamped into the ground by goats (as these animals are the ones which commonly graze in the guayule territories), or had been dropped by these animals and thus found favorable conditions of development in the animal excrements. It would, in fact, be difficult to find any other explanation for the enormous growth of the guayule plant in small, isolated places (having usually the size of the resting-places of the herds of goats) \* \* \*."

As to the supposedly favorable conditions afforded by animal excrement, it may well be doubted that these are more so than the soil itself affords. Experiments have shown that soil at all rich in humus derived from manure is distinctly unfavorable for healthy germination. Even "garden" soil at Cedros, with no addition of manure, is less favorable than the unaltered lime-charged soil of the normal guayule habitat (plate 16, figures D and E). Even after thorough leaching from exposure the possible advantages are hardly important, and, at all events, in such situations the seeds and seedlings have no advantage of shade, as the herding-spots of goats are usually bare of vegetation. Nor can the stamping into the soil by these animals have any value, as the seeds germinate well only with very shallow soil covering, as much as 2 mm. depth being enough to show a marked decrease in germination.<sup>1</sup> It would seem, therefore, that if Endlich's observations are correct as to the occurrence of guayule seedlings in such situations, it is safe to infer that the rainfall conditions are, on occasion, such as to make ready germination and early growth possible for a good percentage of seeds even in open bare spots where no advantage of shade is offered. My own observations, at any rate, sustain this view. Experiment 139 (see p. 72) is a case in point, and the results were supported by general observation during the summer of 1908, when there was a fairly generous if not a maximum field-germination. The net result of this season is indicated by the numbers of seedlings observed in April 1909 (see p. 70). These are known to have germinated at or during the growing-season of 1908, and had successfully sustained prolonged drought till the time of observation. At no other point was there seen a better crop of seedlings at the age of these, and they germinated without the least protection, as the quadrat had been completely denuded.<sup>2</sup>

Nevertheless, when seedlings are observed in the field at other than favorable seasons, it is frequently noticed that the larger numbers are in the protective shade of other plants; but this is not peculiar to the guayule alone. The explanation, we believe, is not that the guayule seedling is ombrophile, but that the eliminating effect of the drought period subsequent to a period of germination is more drastic elsewhere

<sup>1</sup> Kirkwood, 1910.

<sup>2</sup> By contrast, it should be said that at Station 1 only very few seedlings were found on a large area denuded of all plants save small guayule. As goats had been pastured here, however, it is impossible to draw any conclusions.

than in the shade. Thus, in February 1908, small seedlings with 1 to 5 foliage leaves could be found beneath the shade of an occasional larger guayule plant, but in a precarious condition, some dead, others moribund, and plainly the survivors of the crop of seedlings of late in 1907, the chief part of which had succumbed to the very severe conditions already noted as having prevailed at Cedros at that time. As bearing upon this question, we may note the meager occurrence of *Opuntia leptocaulis* in southern Arizona, where it is scarcely to be found except protected by some plant, while it grows in the open in great abundance in Zacatecas. It appears evident that in Arizona the conditions for its persistence, except when it is more or less protected by other plants, are too severe. No such relation has been observed in Zacatecas, and it would seem that the climatic conditions there are distinctly more favorable for this plant.

It would therefore appear safe, if desirable, to clear guayule fields of the major part of other vegetation. An occasional year may be expected when the rate of germination will go far toward producing a good stand of young plants. Those already growing will offer protection to the younger brood, and the larger area available for guayule plants will in part compensate for the loss of shade given by other vegetation. It would not be advisable, however, to remove the occasional palma samandoca (*Samuella carnerosa*), which produces fiber, or the large barrel cacti ("bisnaga burra" and "bisnaga colorada"), as they are heavy plants and neither spread with appreciable rapidity nor occupy more than a negligible fraction of the ground (plate 1, fig. A). This principle of practice is, however, in the nature of a compromise, and rests upon an estimated balance of circumstances. A more correct estimate of probabilities could be based only upon longer observation under experimental conditions.

## RATE OF REPRODUCTION AND OF GROWTH.

### RATE OF GROWTH DURING GERMINATION.

This period may be divided into a period of tissue expansion and one of induration. At the close of expansion, which begins in about a week's time after sufficient rain, and occupies a second week, the seedling is tender, the hypocotyl white and translucent, and the cotyledons green (fig. 8). The cuticle then thickens, and red color is developed in the epidermis of the hypocotyl and under surface of the cotyledons, while the latter become darker green and more indurated. This occupies a third week, when, if no untoward circumstance interferes, the first foliage leaves develop. Even under the best of conditions this period of three weeks will scarcely be shortened.

The further seedling development is a direct function, other things being equal, of the rainfall, the maximum potentiality, it may safely be said, never being exerted by field plants. This apparently extremest limit of growth for a seedling was reached by one of two particular individuals under cultivation, and constantly supplied with an abundance of water. The height of this plant when the rhythm-limit was reached, as indicated by cessation of growth, was 25 cm., and it had a spread of 22 cm. It was a fully-developed specimen, in which each branch reached

its proportionate size. It flowered freely and produced fully 2000 seeds (exp. 139a; plates 18 to 20). The time occupied in its growth was about four months.

We may now offer data (table 27) derived by field observation during the growing season of 1908, which was a favorable year, though not perhaps exceptionally so. The rate of growth during germination is indicated by the measurements of seedlings from Station 3, collected July 15, 1908. They were two to three weeks old.

TABLE 27.—Rate of growth during period of germination.

Hypocotyl		Cotyledon.	
Length.	Diameter.	Length.	Breadth.
mm.	mm.	mm.	mm.
6.5	0.75	3.5	3
6.5	0.5	2.5	2.5
10.0	1.0	4.0	3.5
11.0	1.0	4.5	4.0

Table 28 contains data based upon the individual examination of 112 seedlings collected in the field on the dates mentioned. The measurements are exclusive of the hypocotyl, which measures about 10 mm. on the average.

TABLE 28.—Amount of growth of seedlings in the first season of growth.

Collected.	No. of seedlings.	Height including leaves.			Length of stem.			Locality.	Notes.
		Max.	Min.	Ave.	Max.	Min.	Ave.		
Feb. 1908	11	mm. 17	mm. 7	mm. 10	mm. 2	mm. 0	mm. 1	Loma north of Cedros.	Germinated Nov. (?), 1907. 2 to 5 foliage leaves. Cotyledons long gone. Plants of very slow growth.
June 2, 1908	1		70			30		Station 2....	An exceptional and very large seedling for this date. Inflorescence 2.5 cm. long. Cotyledons still attached. 1 to 7 foliage leaves.
Aug. 8, 1908	28	33	6	20	2	0	1.2	Loma north of Cedros.	Cotyledons still attached. 1 to 7 foliage leaves.
Sept. 8, 1908	24	65	10	35	12	1	5.7	Sta. 8, quadrat 1.....	Good healthy specimens.
Sept. 12, 1908	6	75	47	62	17	5	9.6	Station 2.....	Do.
Sept. 12, 1908	11	90	50	73	50	7	24	Station 2.....	2 in flower. Max. stem diam. 3 mm.
Sept. 12, 1908	31	75	30	45	20	3	9	Bare quadrat in plain between Cedros and Sta. 2.	Good healthy plants.
Grand aver.							14.8		

The seedlings in table 28 were not selected, but were, in each case, all the seedlings found in a given area. Taking those collected in September—which, judging by the behavior of guayule plants in general, was near the close of the growing-season—we have an average rate



of growth of about 14.4 mm. in stem-length (epicotyl), aside from the small secondary branches. With few exceptions, the seedlings of a month previous (August 8) were very small, as indicated in the table, but nevertheless the size attained by them, judging from experience in their culture, must have been the result of at least six weeks' growth.

This was not the close of the growing-season, but I was fortunately able to complement the above data by measurements of seedlings, already mentioned in other connections, which had passed completely through the growing-season of 1908 and been collected<sup>1</sup> in April 1909, in a state of dormancy. The measurements of 311 seedlings were made by caliper.

Tables 29 and 30 give the data for two quadrats; a third, having 281 seedlings, 4 of which are seen in plate 17, fig. A, is not given in detail.

Combining the averages obtained from tables 29 and 30 with the data for Station 3, quadrat 4, obtained at the same time as those of Station 2, quadrat 7, we obtain table 31.

TABLE 29.—*Growth of seedlings which germinated about June 1, 1908, and examined April 2, 1909. Station 3. All within 100 square meters.*

No.	Length of main stem above hypocotyl. (Hypocotyl 10 mm.)	Diameter at base.	Remarks.
	<i>mm.</i>	<i>mm.</i>	
1	35	3.5	Flowered, flower bitten off; branched.
2	19	3.2	Branches 1 to 3 mm.
3	9	2.0	Unbranched.
4	10.5	2.2	Lateral buds just started.
5	11	2.0	Unbranched.
6	11	2.0	Do.
7	5	2.8	Two buds at base of hypocotyl; otherwise unbranched.
8	8	2.0	Slender branch 5 mm. long at base of hypocotyl; otherwise unbranched.
9	6	2.5	Unbranched.
10	4	2.0	Do.
11	5.2	2.0	Do.
12	5.2	2.0	Do.
13	5.0	2.0	Do.
14	4.2	2.0	Slightly damaged; unbranched.
15	4	1.8	Unbranched.
16	3.0	1.7	Do.
17			
18			
19	4.0	1.2	Do.
20	3.0	1.2	Do.
21	2.5	1.0	Do.
22	17.0	0.8	Unbranched; etiolated.
23	8.0	1.0	Unbranched; slightly etiolated.
Ave.	8.1	1.8	

23 seedlings; average length of main stem, excluding Nos. 22 and 23, which are not normal, 7.65 mm.; average diameter of main stem at base, 2 mm.

N.B.—The exact age of the above seedlings does not exceed 10 months. Of this period, 6½ months were without rain, beginning with the middle of September. All the seedlings were alive at the time of collection.

<sup>1</sup> In company with Mr. G. E. Pell, of New York.

TABLE 30.—*Growth of seedlings (all unbranched) which germinated about June 1, 1908; collected April 3, 1909. Station 2, quadrat 7, 100 square meters.*

No.	Length of main stem exclusive of hypocotyl (about 10 mm.).	Diameter at base.
	mm.	mm.
1	4.5	2.0
2	5.0	2.0
3	5.0	2.0
4	6.0	2.0
5	3.5	1.5
6	6.0	1.3
7	5.0	1.0
Ave.	5.0	1.7

TABLE 31.

No. of seedlings in quadrat.	Length of stem.			Diameter of stem.		
	Max.	Min.	Ave.	Max.	Min.	Ave.
	mm.	mm.	mm.	mm.	mm.	mm.
23	35	2.5	8.1	3.5	0.8	1.8
7	6	3.5	5.0	2.0	1.0	1.7
281	55	1.5	12.6	6.0	0.8	2.8
311						
Ave.	32	2.5	8.5	3.8	0.9	2.18

It will be seen that the average maximum amount of growth for the whole of the growing-season of 1908, as indicated by the data obtained in April 1909, is 8.5 mm., stem-length. This, however (as shown by table 28), is less than the amount determined by the measurement of seedlings, germinated in 1908 but collected on September 8 to 12 of that year, namely, 14.8 mm. The difference in favor of the earlier collections may perhaps be explained by the fact that care was not taken to take *every seedling* in a given area. To do this requires a minute search, which was given only in April 1909. It is not improbable also that other seeds germinated later in the season, though this is not likely. It is therefore safer to conclude that the average amount of growth in length of the epicotyledonary stem for the season of 1908, taking *all* seedlings into consideration, is not more than 1 cm. If we should consider only those which germinated at one time, at the beginning of the growing-season, this amount would probably turn out to be somewhat greater. Under the conditions for the period in question the maximum amount of growth was 5.5 cm.; the minimum, 1.5 mm. Seedlings of these dimensions, and two illustrating the average growth of 281 seedlings (Station 2, quadrat 4), are reproduced in plate 17, fig. A. Measurement of the main shoot alone throws out of account the growth of branches, so that a fuller conception of the amount of development possible for a seedling under natural conditions may be had only by seeing the plants themselves.

## RATE OF GROWTH IN MATURER PLANTS BEYOND THE SEEDLING STAGE.

In general forestry practice the use of formulæ is directed toward estimating the amount of lumber in the trunk. The deduction of these formulæ is easier in the case of coniferous trees because of the continuous growth of the chief shoot. Special problems demand formulæ based upon other data than the rate of growth of wood, *e.g.*, in the business of producing cork from *Quercus suber*. When forestry practice is directed toward the culture of camphor trees, for example, in which the whole bulk of the plant is to be used, the desideratum will be to determine the rate of increase of weight. This is the case with guayule, since the whole of the plant is used in the process of extraction of crude rubber. But the rate of increase in weight can not be determined without introducing the time element, so that we must first determine the rate of stem elongation in order to arrive at a general average of growth. But plants of the same age are not invariably, or even quite usually, of the same weight, since the relation of a plant to its environment results in more or in less bushiness, in partial death and consequent loss of branches, in unusually slow or rapid growth, or in total loss of plant by death. In estimating the weight of shrub per unit of area for some future time it is evident that all these factors are disturbing elements, the values of which may not be easily determined. About the best we can do, therefore, is (1) to determine the average rate of growth in length of stem, and (2) to determine the rate of increase in weight for critical periods. The data indicate that there is a period of relatively highest growth-rate, expressed in stem length or height, and a period of relatively greatest increase in total weight of the plant.

## RATE OF GROWTH IN TERMS OF STEM-LENGTH.

It has already been shown that the first season's growth results in an average stem-length approximating 1 cm. A stem of this size has no branches. During the second season's growth the stem may simply lengthen, or it may also produce a number of short branches. This it is more certain to do if the chief shoot produces an inflorescence. It may otherwise merely elongate strictly for a number of years, resulting in a very slow increase in weight, since the weight is affected chiefly by the number of branches. At best the total weight assumed by a plant in the first 7 to 10 years is small, seldom exceeding a few ounces.

## RATE OF GROWTH IN EARLIER YEARS AFTER GERMINATION.

To determine precisely the age of a given seedling is more difficult than would seem at first glance if it has been exposed to the weather for more than a year. Furthermore, the rate of growth in many individuals is so slow that the marks become well-nigh effaced, if not quite so. In obtaining the following measurements, only plants which showed the markings plainly enough to be seen clearly have been used. This has very naturally thrown out those of very slow growth, in which the difficulties are greatest, and thus the resulting average datum is probably too great. By way of orientation two extreme cases may be cited. One is a seedling of two seasons' growth, which germinated in 1907, making



in that year 3 cm. and in the following year 11 cm., a total of 14 cm. in the two years. This is the largest field plant for its age that I have seen. In contrast is cited a seedling of slow growth, fully 7 years of age, entirely without branches, and only 6 cm. in height. The average rate of growth falls between these extremes, but nearer the lower. For the sake of brevity, as it would serve no useful purpose to introduce large tables of figures, the summaries of measurements alone are given.

The average rate of growth of 30 seedlings from 2 to 5 years old during particular years is as follows:

TABLE 32.

Age.	1908.	1907.	1906.	1905.	1904.	Average amount of growth.
	mm.	mm.	mm.	mm.	mm.	
2	15	16	..	..	..	In first year, 17 mm.
3	45	22	20	..	..	In second year, 20 mm.
4	51	30	24	15	..	In third year, 37 mm.
						In fourth year, 51 mm.
						31 mm.

The average amount of growth in seven seedlings for the last three years, 1906-1908, is 26 mm.

Some ten seedlings for each of the localities mentioned below were measured, giving average amount of growth for two to four years, as follows:

	mm.		mm.
Sierra Candelaria.....	22	Cerritos de los Calzones.....	20
Station 4 (Sierra Guadalupe) .	24	Cedros.....	34
Station 5 (Sierra Guadalupe) .	18	Apizolaya.....	42
Station 2 (Sierra Zuluaga).....	31	Lomerio de los Zorrillos.....	49
Station 2 (Sierra Zuluaga).....	40	Encarnación.....	26
Station 1 (Jagüey).....	30	Average rate for all.....	30

It will be seen that these figures, made at different times on material from different localities, check each other fairly well. As said before, the average rate of growth thus deduced is probably somewhat high. The rate undoubtedly increases toward the fifth year, and a somewhat more rapid rate is then maintained during a few years, say from the fourth to the seventh, during which the total height of the plant increases at a greater rate than before or after. Usually during the second or more frequently the third year a set of branches start their growth, and with this the weight increases more rapidly. What this weight may amount to in four years is shown by 3 thrifty plants taken on the Lomerio de Zorrillos. These made growth as follows:

TABLE 33.

1905.	1906.	1907.	1908.	Dry weight.
mm.	mm.	mm.	mm.	grams.
10	35	60	10	12
20	50	84	40	30
20	40	160	20	30

Hence we may conclude that the weight gained in four years' growth can scarcely exceed 1 ounce, and probably seldom amounts to that.

The following are measurements (in millimeters) from rapidly growing plants from Station 2, collected in January, 1908:

TABLE 34.

Plant.	1902.	1903.	1904.	1905.	1906.	1907.	Notes.
		mm.	mm.	mm.	mm.	mm.	
1 {	..	40	30	94	32	40	} Average height from base of 1904 growth, 210 mm. Weight 17 gms.
	..	40	25	76	35	20	
2 {	..	..	16	84	65	45	} Average height of twigs 194 mm. Weight 12 gms.
	..	..	16	80	100	50	
3	..	..	17	34	67	10	Habit strict, with short branches above. Weight 5 gms.
4	20	30	40	70	25	25	Not less than 6, possibly 7, years old. Height 200 mm. Dry weight 47 gms.

It is of interest that plant 4, though a slower grower in height than 1, made weight about twice as fast. This is due to the larger number of twigs. Plant 4 may be regarded as an expression of the best results which may be expected in this station. We may therefore conclude that the weight of 4-year-old plants will not on the whole exceed 15 grams or 0.5 ounce, and that the maximum weight for a 6-year plant will not exceed, say, 45 grams or 1.5 ounces.

#### RATE OF GROWTH IN MEDIUM-SIZED PLANTS.

As in the case of seedlings, the annual accretions of growth have been measured only when sufficiently clear for certain recognition. The last 2 to 5 or more years' growth was measured, according to the visibility of the markings. Several hundred measurements were made in all, of which the summaries and averages alone are given in table 35.

TABLE 35.—Average amount of growth per year in the localities indicated.

Locality.	Average amount of growth.	Locality.	Average amount of growth.
	mm.		mm.
Sierra Candelaria.....	44	Cedros.....	56
Station 1 (Jaguey).....	30	Apizolaya.....	42
2 (Sra. Zuluaga).....	31	Lomerio de los Zorrillos.....	49
4 (Sra. Guadalupe).....	41	Encarnación.....	28
5 (Sra. Guadalupe).....	38	Caopas.....	31
Cerritos de los Calzones.....	182		
		Average of all.....	43

<sup>1</sup>NOTE.—The plants in this locality showed very rapid growth in 1906, explainable by the rain and by their having been previously cropped back. The branches were few in number, so that the plants, though relatively tall, were very light in weight. This figure would therefore better be thrown out of account, in which case the average falls to 38 mm. per year. The datum for Station 2 has been checked up by a later count, 26 measurements giving an average of 32 mm., and at this point it may be said that the data above given are collated from measurements made at different times, results being used as checks, the one on the other.

In addition to data obtained by observation of external marks, a number of measurements of field plants were made by the usual laboratory method of marking the stem with India ink. The results of these observations are here given:

*Station 2, quadrat 3.* 6 twigs marked at the tip with a drop of ink, Jan. 6, 1908. Growth commenced Apr. 28. Last observation Apr. 3, 1909. Measurements as follows, in mm.: 60, 75, 70, 75, 65, 50. Average amount of growth for season, 66 mm.

*Station 1.* 5 plants marked Jan. 3, 1908. Last observation made Apr. 3, 1909. The mark had been destroyed on 2 plants. The total amounts of growth for the 3 remaining were 30, 18, and 35 mm., making an average for the 3 of 28 mm. All growth was subsequent to May 29.

*Station 3.* Dec. 31, 1907. 3 marked plants showed an average growth of 1 to 2 cm. A seedling slightly pruned showed 2 cm. new growth by July 15. The rate of growth in all plants at this station was small in 1907.

*Station 6, a low gravelly ridge in the playa, Burrita.* 4 plants marked Oct. 11, 1907. On Jan. 11, 1908, 2 plants showed 1 mm. and 2 plants 2 mm. growth each. The total amount of growth till Aug. 21, 1908, was 13, 20, 20, and 10 mm., or an average amount of 18 mm. This is a locality of conspicuously slow growth.

The average amounts of growth observed in marked plants for the season of 1907 were, therefore, 66, 28, 20, and 18 mm., making a grand average of growth of 31 mm. The average is lower than the one above deduced from measurements of field plants, but as three of the stations suffered severely from drought in 1907 the rate of growth was probably rather low. Our data on the whole indicate that the rate of growth of guayule in the field lies somewhere between 30 and 40 mm. annually. This general conclusion can scarcely be said to be too optimistic. It will no doubt be questioned by those who entertain different ideas of the rate of growth of this plant. The belief is current in many quarters in Mexico that growth is much more rapid, it being a common saying that after guayule has been cut the crop is reestablished in five years. Such surprising statements were made to me regarding one locality in particular that I made special effort to obtain evidence. Although an attempt to visit the place, some leagues to the west of Escalon in Chihuahua, was frustrated, I succeeded, through the courtesy of some friends, in getting a number of plants, which, though of somewhat more rapid growth than usual, are not remarkable in a special degree. The plants were clean-limbed and smooth-barked, the effect of this more rapid growth. They bear evidence of a heavier rainfall as compared with plants from Zacatecas, but this appearance is due in part to the fact that they are of two different types; in one the foliage shoot is abruptly terminated at the base of the peduncle; in the other the shoots taper out into the peduncle after the fashion in mariola. The branches in the latter are thin, die back readily and often for a good distance, and in these plants have some of the characteristics seen in the stems of irrigated plants. I give measurements of the few plants, which came to me for study, in detail (table 36).

The average amount of growth of each plant for the years indicated is: plant 1, 30 mm.; plant 2, 41 mm.; plant 3, 37 mm.; and for all the twigs on 3 well-developed plants of the first-mentioned type, viz, with abruptly ending foliage-shoots, it is 37 mm. The data are instructive in that they point to a "fat" year preceding two "lean" years, namely, 1907 and 1908. The rate of growth, however, compares very closely with that derived from material from other localities.



TABLE 36.

Plant No.	Branch No.	Amount of increase in stem length for—			
		1905.	1906.	1907.	1908.
No. 1, 85 cm. tall, dry weight 5 lbs. 5 oz., symmetrical, well developed.	1	mm. 62	mm. 41	mm. 8	mm. 8
	2	..	42	18	10
	3	45	57	10	4
	4	..	..	25	18
	5	..	26	11	16
	Average.....	53	41	14	11
No. 2, 60 cm. tall, dry weight 2.5 lbs., irregularly developed.	1	..	117	10	20
	2	..	..	86	15
	3	..	..	77	28
	4	..	80	22	18
	5	..	55	16	20
	6	..	65	10	10
	7	..	80	23	13
	8	..	57	8	10
	Average.....	..	76	31	17
No. 3, 35 cm. tall, dry weight 9.5 oz., 10 yrs. old, well developed, symmet- rical.	1	50	60	17	25
	2	50	70	20	10
	3	55	62	17	25
	4	60	70	7	8
	5	25	90	15	15
	Average.....	48	70	15	17

TABLE 37.

Plant No.	Branch No.	Amount of increase in stem-length for—		
		1906.	1907.	1908.
No. 4, seedling 23 cm. tall, weight 10 gms.	mm. 1	mm. 57	mm. 90	mm. 24
No. 5, 38 cm. tall, weight 48 gms. ....	1	60	48	90
	2	..	36	46
	3	..	45	70
Average.....	..	60	43	69
No. 6.....	1	50	15	50
	2	60	30	60
	3	..	23	40
	4	..	15	60
	5	65	12	6
	6	20	8	30
	7	30	15	45
	8	80	30	30
	9	35	25	75
Average.....	..	47	19	44
Average for all years.....	..	37		

Table 37 gives measurements for the years indicated of 3 "spindling" plants, which grew rapidly in height but did not develop branches and therefore weight.

Plant 7 was 50 cm. tall and weighed 153 grams, ragged, but showing abnormal development on certain shoots. The last three years of its growth showed accretions, a side-shoot starting low down, of 110, 200, and 60 mm. The upper shoots appeared quite similar to those of the other plants, but were more or less damaged, so that one could not get satisfactory measurements.

The conclusion one is forced to draw from a survey of the above tables is that in a certain proportion of the plants in the locality referred to the rate of growth per year approaches closely to 50 mm. In these plants, however, the branches are thin, and the plants are not well developed nor heavy for their size, so that, economically considered, there is nothing gained. Whether the differences in rate of growth are connected with racial differences in the plants is discussed elsewhere.

#### RATE OF GROWTH IN IRRIGATED PLANTS.

A considerable number of plants were under observation for the whole of two growing-periods, during which time they were freely irrigated<sup>1</sup> and grew rapidly, at a rate close to the rhythmic maximum. The average rate of growth for the two years was very close to 25 cm. per year, so that a spread of a meter was attained by nearly all of the plants. The character of the growth is described elsewhere, but the fact here stated indicates very clearly that plants in the field may never be expected to reach this maximum. The greatest growth of stem-length in field plants for one year, 200 mm., was seen in a very few twigs and in shoots favorably placed, the rest of the plant failing to behave similarly.

The weight attained in two seasons by irrigated plants growing from small butts after transplanting is upwards of 2 pounds, or slightly over. The fresh weight of a large plant was 4.5 pounds. Another collected at the same time weighed fresh 3.5 pounds, and shrank in drying to 1 pound 10 ounces. The dry weight of two others was 28 and 32 ounces.

On the other hand, plants under limited irrigation were grown at Caopas. I have examined three sample individuals of these, a large, a medium-sized, and a small plant. All of these failed to start promptly, and had been pollarded. The amount of growth made by them is shown in table 38.

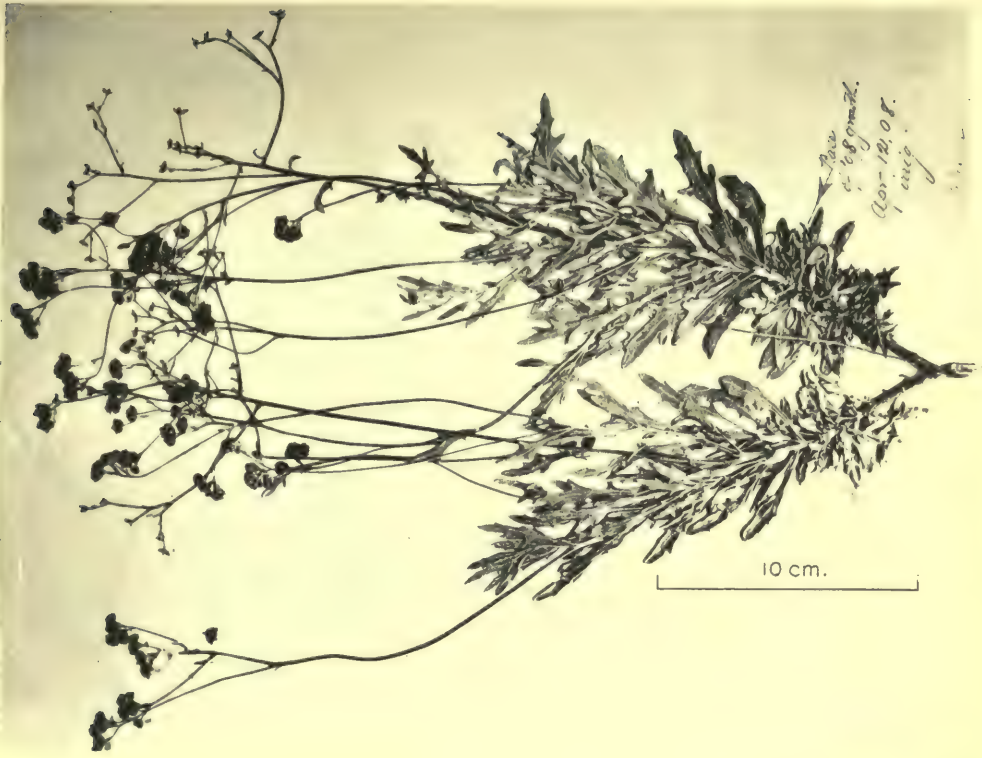
TABLE 38.

Size of plant.	Distance pollarded above ground.	Amount of growth.		
		1908.	1909.	Total.
	cm.	cm.	cm.	cm.
Large.....	40	11	9	20
Medium.....	30	16 to 18	10 to 12	25 to 30
Small.....	15	13	8	21

<sup>1</sup> In 1907, through the winter until the following April. They were not irrigated later, but received rain in the summer. They had a sufficient amount of soil-moisture for continuous growth.



A. A branch, one year's growth under irrigation.



B. A branch in the height of flowering, second season.





The smaller amount of growth in 1909 was due to the absence of irrigation, as elsewhere explained. It will be noted that the medium-sized plant responded best, which in general comports with our observations of the rate of growth of field plants.

#### GENERAL CONCLUSIONS.

The maximum rate of growth of guayule under irrigation is in the neighborhood of 25 cm. per year stem-length. The amount of growth between the field average and the maximum average for irrigated plants may be closely regulated by irrigation, to which the plant readily responds.

#### FIELD PLANTS.

When it is borne in mind that the total height of a plant is, except in young seedlings of strict habit, always less than the sum of its longer annual growths, because of (a) partial dying back and (b) the branching habit; and when also it is remembered that numerous plants suffer from untoward conditions, either by the depredations of parasites or from poor soil-conditions, it is not far from the truth to say that the average annual rate of increase in height is 3 cm. A plant 30 cm. in height would therefore be 10 years old. Plant 3, above described (p. 83), which has undoubtedly a higher rate than 30 mm. per year, is, as certainly as may be estimated, 10 years old. As has been said previously, however, the important desideratum is to determine the period of life during which the increase in weight is most rapid, aside, of course, from the very young seedling stages, when the ratio of increase may be rapid, but the total weight very little. For the purpose of arriving at this information, I have assumed the rate 3 cm. per annum as a constant factor. A large number of plants have been weighed and measured, and the data thus derived have been correlated so as to obtain curves of increase in weight according to size (fig. 13). For the data the reader is referred to tables 4 to 13.

The curves have not been constructed for plants over 40 cm. in height for two reasons: the number of plants beyond this size is very much smaller, and, again, their age is too great to admit them to a practical consideration of rotation periods. Observations from which, in part, the tables of data used in the construction of the curves have been derived, all go to show that the first pronounced gain in weight is entered upon after the plant has reached a height of 30 cm. The average weight of plants of this height is somewhat over 5 ounces, ranging chiefly between 2.5 and 8.5 ounces. The average weight of plants 40 cm. tall is, on the other hand, 15 ounces or more. That is, the average weight is trebled in making the 10 cm. advance in height beyond 30 cm. This is shown in the positions of the curves, which, however, present more irregularities than one would wish, in spite of the fact that they are based on measurements of several hundred plants. The greatest fluctuations in the curves are caused by the introduction of exceptional individuals, for where larger numbers are used the curves are more uniform. The exceptional individuals may be either "spindling" or unusually well-developed in point of ramification.

## AGE AND HEIGHT.

For the purpose of controlling the above conclusion I have, as clearly as possible, made estimates of the ages of plants of various sizes, making no assumption as to the rate of growth, but being guided solely by the marks in each individual. The results are compiled in table 39.

TABLE 39.—Size, weight, and closely estimated ages of guayule plants.

Series.	Height.	Weight.		Age.	Remarks.
		Fresh.	Dry.		
	cm.	oz.	oz.	yrs.	
I	35	..	10.75	11	Very well developed, symmetrical.
	30	..	5.0	8	Medium, rather undersized.
	28	..	4.5	7(8)	Normal.
	25	..	4.0	7	Do.
II	17	..	0.875	6	Do.
	51	18	11.6	14	Y-shaped, symmetrical. "Macho."
	35	8	4.0	10	Do.
III	50	12	6.7	10 to 12	Y-shaped, symmetrical. "Hembra."
	30	6	3.25	7 to 8	Do.
IV	66	32	24.0	19 to 20	Y-shaped, narrow-leaved type.
	40	7	4.5	10 to 12	Do.
V	40	10	6.0	15(?)	Slow-growing, broad-leaved type.
	35	5	3.06	12	Do.
VI	50	54	36	17 to 20	Densely branched, spreading, in full leaf.
	45	44	29	16 to 18	(NOTE. Plants of series VI are the heaviest for their height of any, except very occasional plants such as that in plate 8, fig. B.)
	33	16	14	10 to 11	
	21	6	5	9	
	20	5	3.75	8	
	15	1.75	0.93	6	
VII	65	64	43	20	V-shaped, half-spreading type, densely branched, symmetrical (plate 8, fig. B).
	55	32	18	15 to 16	
	50	18	15	13 to 15	
	33	8	5.5	9	
	28	6	4	8	
	24	3	1.5	7	
VIII	22	1.25	0.5	6	
	55	18.5	..	15 to 16	Y-shaped (plate 8, fig. A).
	30	6	..	11	Normal shape for age.
	25	1	..	9	Do.
	20	0.875	..	7	Do.
	14	0.5	..	5	Do.
	4.5	0.1	..	2	Do.

These data have been charted in the accompanying curves, correlating age and height (fig. 15, upper diagram). It is an obvious objection to the value of these curves that they are based, necessarily, on comparatively few plants, but their value is enhanced by the individual treatment, since the estimate of age was made with great care. A fairly close correlation emerges, however, from the diagram, from which we see that plants of 10 years of age have a height of about 30 cm., and those of 15 years about 40 cm.

An increase in height of 10 cm. over 30 or 35 cm. is correlated (judging from the data of table 39) with a doubling at least of the weight



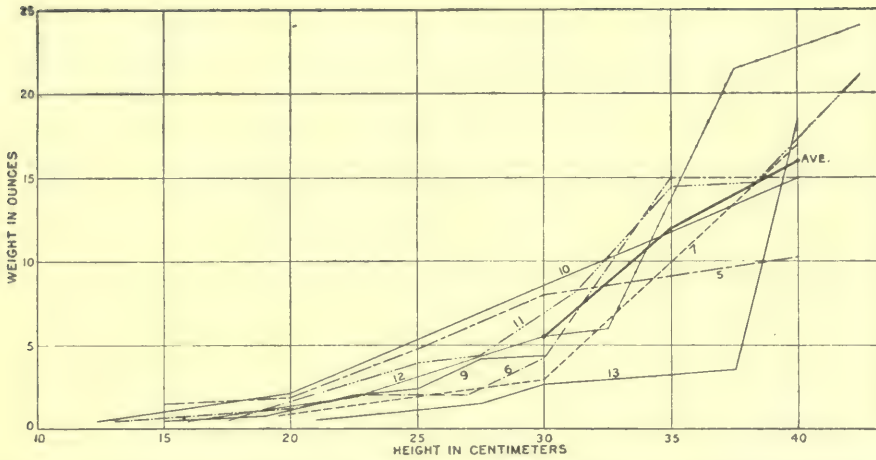


FIG. 13.—Curves correlating height and weight in the plants recorded in tables 5 to 7 and 9 to 13, inclusive. The approximate averages are indicated in the curve of averages.

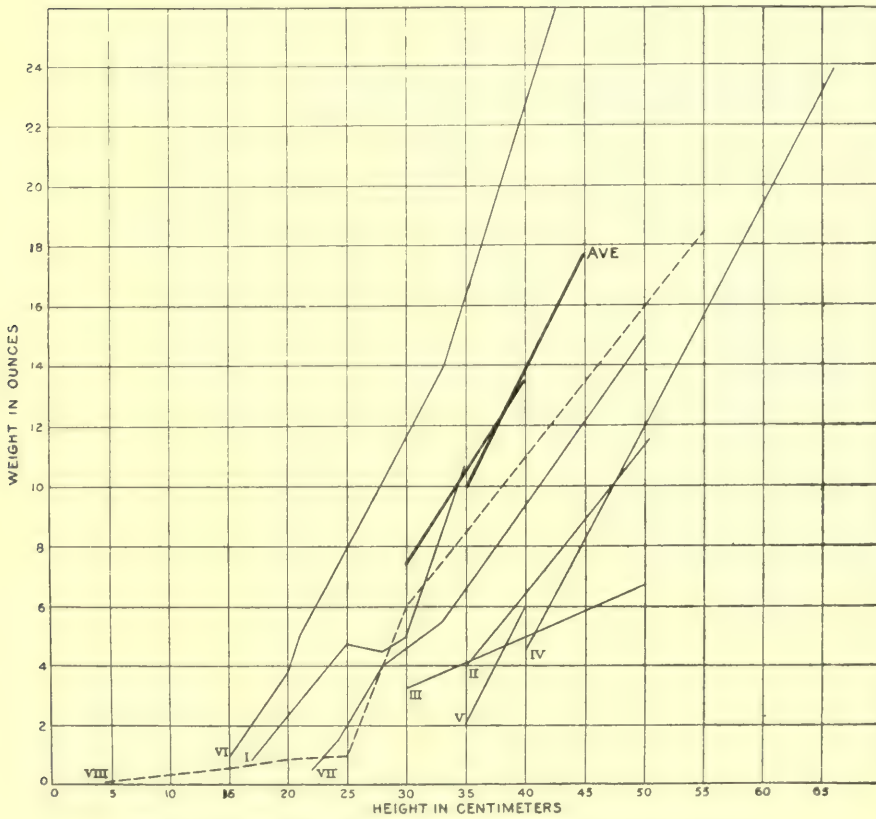


FIG. 14.—Curves correlating height and weight of the plants in table 39.

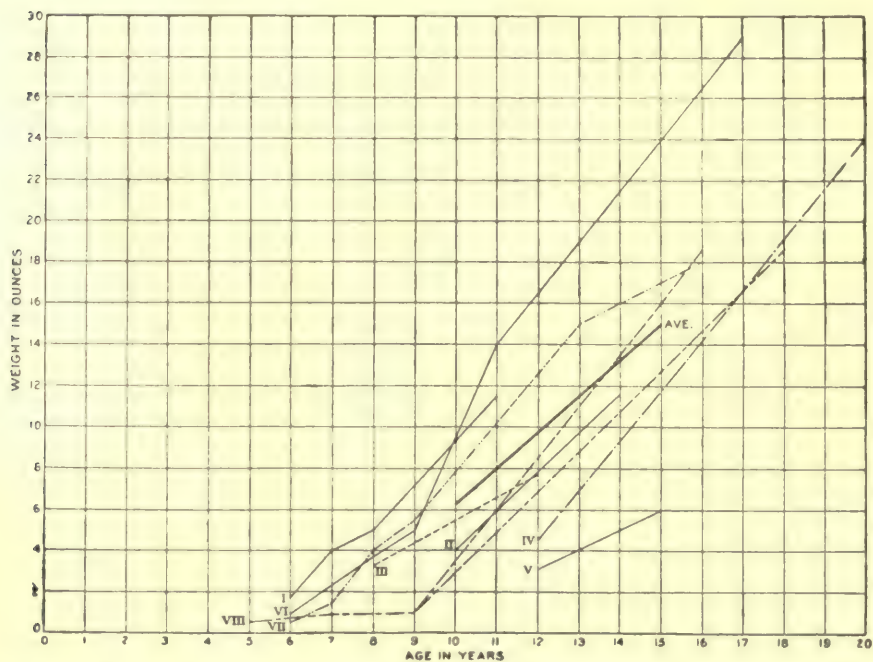
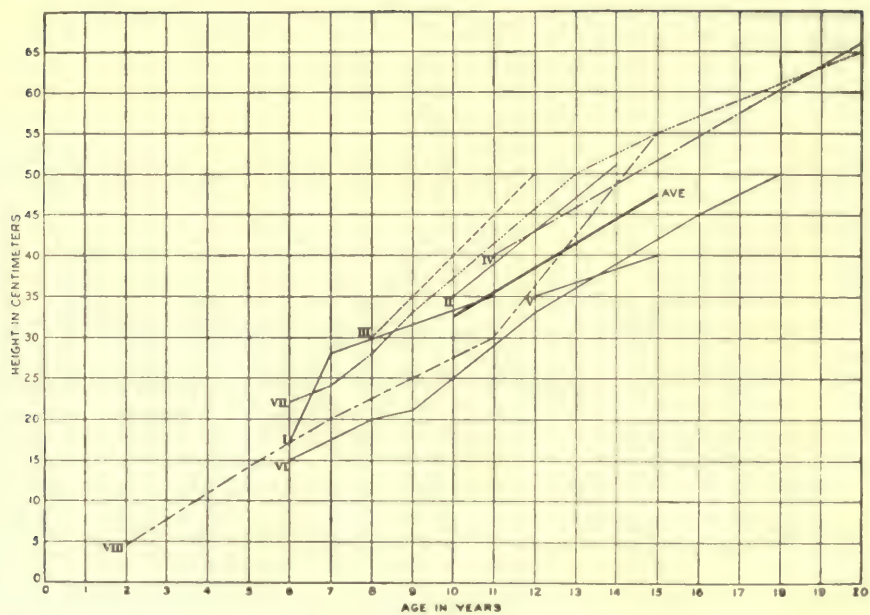


FIG. 15.—Upper diagram: Curves correlating age and height of plants in table 39. Lower diagram: Age and weight correlated. The same plants.

(fig. 14). Fig. 13, on the other hand, indicates a greater increase, to nearly three times the weight at 30 cm. The average weight of a plant 30 cm. in height is, according to fig. 14, about 7 ounces, but as the plants considered in this curve are normally developed or indeed considerably above the average, the average weight of a 30 cm. plant is probably nearer to that indicated in fig. 13, viz, 5 ounces. The mere ratio of change in weight is not peculiar to these dimensions alone. What appears from the data is that the weight of plants up to the height of 30 cm. is not great enough for economical harvesting. The increase in size and weight, however, is as great in the subsequent five years as in the previous ten, so that taking the crop at the end of ten years would give results only half as great as the returns of a fifteen-year rotation period.

This conclusion is shown graphically by fig. 15, lower diagram, which indicates that the weight of a plant advances from about 6 ounces at ten years of age to 15 ounces at fifteen years. A considerable minus error in the estimation of ages might be allowed, and yet the increase indicated in the preceding paragraph would still be shown. It is fair to state, however, that there is little chance for such error, as I have taken the precaution of being conservative when there was doubt.

Fig. 15, upper diagram, indicates that the estimate of rate of growth used throughout, viz, 3 cm. per year, is very nearly correct. We may therefore conclude:

- (1) That the average rate of growth of guayule per annum is about 3 cm.
- (2) That the amount of increase in weight between the tenth and fifteenth years of its age is at least as great as that occurring during the first ten years; and that this further justifies, from an economic point of view, a fifteen rather than a ten year rotation period, aside from considerations which might be drawn from loss by death (p. 71), could we ascertain this accurately enough.



## CHAPTER V.

### ANATOMY AND HISTOLOGY.

While the anatomy of the Compositæ has been studied in much detail, beginning with von Sachs, followed by van Tieghem, Vesque, Vuillemin, Col, and less voluminously by other writers, that of the genus *Parthenium* had, up to 1901, received no examination. In that year the plant which supplies the object of the present treatise came to the attention of the French botanists MM. Fron et François (1901), who gave a brief account of the more obvious features of the anatomy of the stem and of the structure of the fruit. A more extensive paper was published in 1908 by Dr. H. Ross, who visited Mexico in 1907 and examined the guayule in the field, chiefly about Saltillo. In this paper an anatomical study of guayule was supplemented by brief reference to two other species, *P. incanum* and *P. tomentosum*. To both these contributions, as also to those of more general import, reference will presently be made.

#### ROOT.

##### PRIMARY STRUCTURE.

The primary root is diarch. The two bundles of protohadrome, of spiral vessels, become early united by a centripetal development of vessels forming a primary plate, on either side of which stand the two protoleptotome strands. At this time the stele has a continuous pericambium and is surrounded by a well-marked endodermis, which may be recognized by the bands of Caspary and by the starch-content of the cells (plate 22, figs. 6-8). The starch-grains are relatively large and are compound. Their persistence is variable, traces being visible for some months in some instances, *e.g.*, in a root 4 mm. in diameter; in other cases they may have disappeared in a few weeks. Thus in a root 0.46 mm. in diameter, in which radial thickening of the endodermis had just commenced, starch in these cells fluctuates, there being now more and now less, apparently according to the draft upon it by the tissues. Without the endodermis lie three layers of cortical cells with extensive intercellular spaces, which, however, do not occur between the outer layer of cortical cells (the hypodermis) and the epidermis.

##### SECONDARY STRUCTURE.

The epidermis begins very early to break down, so that in a root less than 0.5 mm. in diameter the earliest peridermal divisions have set in. These do not usually occur in the outermost cortical cells, which here take on, in a weak fashion, the characters of an exodermis, as described for *Cephalanthus* and *Tecoma* by Holm (1907), but in the second hypodermal layer (plate 22, fig. 7). At this time growth commences in the cortex, both radial and periclinal divisions occurring (plate 22, fig. 8). Growth of the endodermis is concurrent (plate 22, fig. 6). Both radial and

tangential increase in size results in (1) extension of the radial dimensions of the so-placed walls. This extension is confined to that part of the wall between its outer limit and the band of Caspary, leaving this band in the same position as before (plate 22, figs. 6, 8). With this fact in mind the endodermis may be identified for a long time, indeed frequently till it is well-nigh expelled by secondary thickening. (2) Tangential growth is accompanied by cell-divisions in the radial direction, Casparian bands being formed in the new walls (plate 22, fig. 6). In particular positions, namely, opposite the leptome bundles, the earliest<sup>1</sup> resin-canals appear.<sup>2</sup> These do not belong to the primary structure of the root, but arise secondarily in the endodermis (plate 22, figs. 1 to 5). Their mode of development is as follows: 3 or 4 adjacent cells divide by periclinal walls, thus bringing it about that two or three places occur where 4 cells lie with their angles adjacent. Here the walls split apart, making a simple, prismatic, inter-cellular space without demonstrably different contents; the adjacent cells divide radially, so that each canal has now 4 cells contingent upon and peculiar to it. Later, further divisions, roughly parallel to the early canal-walls, result in the canal consisting structurally of two layers of cells constituting a prismatic tube. It is seen that the endodermal canals, for so they will be called, are arranged in two groups, of usually two or often three or occasionally even four canals each, each group being placed opposite a primary leptome bundle. This relation was first described by von Sachs for *Helianthus*. The structure of these canals does not change, though there ensues some displacement of the cells in roots which have thickened abnormally without losing the outer primary tissues. The figures displaying the cell lineage will make this clear (plate 22, figs. 1 to 5).

The growth of the endodermis may be followed till it is thrown off by the formation of cork within it. During its history it enlarges from a cylinder, of 0.1 mm. inside diameter, of 18 to 20 cells, to one of 3 mm. diameter, composed of hundreds of cells, or even to larger dimensions, before being finally cut out. Throughout the greater portion only radial divisions occur, though the cells increase in radial depth. In the region of the canals, however, the endodermal cells divide in a general periclinal direction, giving rise to two or even more irregular series of cells.

In the ultimate condition of the endodermis and of the secondary cortex the walls of the cells are reticulately thickened (plate 22, fig. 15), so that in a root 2 mm. in diameter, of a field seedling, the endodermis may be followed all the way around with great ease, provided that the rubber has been previously extracted. The reticulations are the result of the oval form of the broad, shallow pores, which are somewhat crowded. They are more strongly developed in plants grown under normal conditions, as appears from the fact that in an irrigated seedling, with a root

<sup>1</sup> Ross (1908, p. 25), in stating that there are only a few canals in the primary cortex of the root, does not make it clear that he refers to canals of endodermal origin.

<sup>2</sup> Exceptions occasionally occur in which the canals in one half-circle of the hypocotyl do not approach on entering the root, and conversely, cases occur in which the grouping of the canals occurs in the hypocotyl, on one side of it. In other words, the root-structure is taken on at a higher level on one side than on the other.

4 mm. in diameter, the reticulations were much less marked or absent. The same condition is found in the definitive stem.

This large size of the cylinder of tissue inclosed within the endodermis is attained only under an abundant water-supply and other conditions insuring rapid growth. Under such circumstances the structure of the canal itself passes beyond the normal definitive stage, and the cells, usually and normally eight in number in transverse section, may suffer further divisions as shown in plate 22, fig. 5, to an extent sufficient, together with some displacement, to render it somewhat difficult to exactly delimit the structure. In a root of this size, viz. 4 mm. in diameter, the endodermis may still be readily recognizable (though irregular in character, being in part of two rows of cells) by the starch-content or by the Casparian spots, or both. The position of the endodermis is always clearly shown, other signs failing, by the primary canals.

The physiological changes in the endodermis are of particular interest. Reference has been made to the variableness of the starch-content of its component cells. When grown under irrigation the starch may be seen in much larger plants than in those which have grown under normal or field conditions. In these growth is less rapid and the extension of the tissues correspondingly less marked. In these also the secretion of rubber ensues earlier and is correlated with the occurrence of drought. In such plants the cells of the endodermis, together with others to be noted below, secrete rubber, so that, in a small seedling with a tap-root 2 mm. in diameter, the cells of the endodermis will be found engorged with this substance. The cells of the canals are especially noteworthy in this respect. By taking advantage of the effect of water upon the rate of secretion, it may be shown that the secretion of rubber in the endodermis takes place first in the cells of the resin-canals (plate 41, fig. 6). Thus, in the root, 4 mm. in diameter, of a seedling which grew with great rapidity, the canal calls were half-filled with small droplets of secretion which reacted to alkanet. The specimen had previously been freed from alcohol-soluble substances, and there can, I think, be no doubt of the nature of the material in question.<sup>1</sup>

The behavior of the pericambium in the region included between the primary leptome and the endodermis differs from its behavior elsewhere. One finds, in a root 1.2 mm. in diameter, that the pericambial cells have enlarged radially and have in some cases undergone periclinal divisions and the daughter-cells further radial divisions (plate 23, fig. 4). The periclinal divisions suggest initial cork-divisions, but this is not the case, as both the radial divisions and the further behavior of the cells show. With a slight increase in thickening in the root, sufficient to attain 1.5 mm. in diameter, the cell-walls are a little thickened and a rearrangement has taken place. The cells have apparently been compressed between the primary leptome and the endodermis, and, under suitable conditions, as in the specimen from which plate 22, fig. 5, was made, have secreted rubber,

<sup>1</sup> I have noticed that reaction to alkanet, which is the same in all the cells at first, becomes in the canal-cells darker with time, the preparation having been kept in darkness. I have attributed this, with some doubt, to the greater protoplasmic content of these cells. Great care was taken to extract very thoroughly with absolute alcohol, and, in a part of my preparations, with caustic potash also.



though less than in endodermal cells with which they are in immediate contact. Further development sees the collapse of the pericambium cells (plate 22, fig. 6), and, as seen elsewhere, the primary stereome occurs in the primary leptome just within the pericambium.

The primary cortical cells outside of the endodermis are also capable of secreting rubber. That they do so at all is contingent on the rate of growth of the seedling. If this is rapid enough to remove the cortex before drought sets in, no appreciable secretion will have occurred. If, however, the rate of growth is lower, so that for the greater part of a year the tissue in question remains functional, the inner cells at least may be found densely filled with rubber. In the root, 5 mm. in diameter, of a field seedling fully a year old, the following measurements (along a radius) were made, from which an idea of the amount of primary cortex remaining active may be had: Wood, 1.4 mm.; secondary cortex, 0.64 mm.; primary cortex, 0.15 mm.; cork, 0.27 mm.

#### EARLY SECONDARY CHANGES IN THE STELE: (HADROME).

With the completion of the primary hadrome plate there ensues a centrifugal development of this tissue by the direct transformation of the protogenic cells adjacent to the middle part of the plate. The increase of hadrome extends along all radii except those lying near the plane of the primary plate, but usually rather less rapidly toward the primary leptome, so that in transverse section there appear two wings, so to speak, of hadrome. This is protogenic, but is added to quite soon by the activity of a cambium which first becomes apparent within and close to the primary leptome bundles (plate 22, fig. 10), and extends toward and finally around the outer edges of the primary hadrome (plate 22, figs. 9 to 10).

Up to this point in the development of the stele nothing exceptional is seen. The only question which has been raised is in regard to the precise origin<sup>1</sup> of the earlier formed secondary hadrome elements, whether this is by means of the cambium which arises on the inner surface of the primary phloem, or is directly from protogenic elements lying adjacent to the primary hadrome plate. The evidence from the material here under discussion is that the latter is the case.

Now, however, a behavior ensues which is somewhat unusual. Two independent mestome strands of (at first) a single radial series of vessels and a very small leptome strand arise, each, usually, in immediate contact with the primary trachea (plate 22, figs. 9 to 11). The emergence of a secondary root disturbs the exact position so that the earliest vessels may be somewhat removed from the primary hadrome. A similar condition has been observed by me in *Lamium amplexicaule*, and by Petersen<sup>2</sup> in other Labiatae.

It is necessary to note that although these mestome bundles are vertically below the two lateral cotyledonary traces, we shall presently see that they are independent of these and have no connection whatever with them.

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<sup>1</sup> De Bary, Comparative Anatomy of the Phanerogams.

<sup>2</sup> I have not seen this paper, but am informed by Dr. Holm.

The appearance of the stele is now suggestive of a tetrarch structure and is as follows: In a plane at right angles to the primary hadrome plate lie the two leptome bundles, between which and the hadrome plate the primary cambium lies. In a plane coincident with the hadrome plate and just beyond its edges lie two small secondary mestome strands, formed independently. These, which I shall here call the intercalated strands, lie, therefore, in a plane between the two broad primary medullary rays (plate 22, fig. 10). The isolated condition of the intercalated bundles is, however, very transient, since the parenchyma rays between the axial hadrome strand and the small intercalated bundles are soon bridged over, the whole, save as mentioned in the following paragraph, coalescing to form a single axial strand of hadrome. Additional secondary bundles are intercalated between those already present, at first from the four angles of the hadrome wings, so that in a tap-root 1.2 mm. in diameter before me (plate 40, fig. 1) there appear 8 bundles, though it must be said that the appearance of the stele in roots of the same size is not by any means uniform.

The closure of the hadrome wings by meeting the xylem of the intercalated strands is not complete, and thus are left two islands (analogous to medullary spots) of unligified cells about the edges of the primary hadrome plate (plate 22, fig. 11). The outlines of these islands are quite irregular, and they may ultimately become compressed or lignified, so that it is only with difficulty that they may be recognized. In thin roots, as especially in the fibrous laterals, the wood cylinder is very compact, and may have no parenchyma rays. In such also the secondary changes in the cortex are less extensive, and the pericycle is much compressed.

#### LATER SECONDARY CHANGES: (CORTEX).

With age the walls of the cortical cells become somewhat thickened and pitted. The intercellular spaces are very regular in shape, and regularly disposed. In a tangential section they appear very uniformly lenticular (plate 28, fig. 5).

#### STEREOME AND SECONDARY CANALS.

Aside from the secondary increase of wood and bast, the appearance of stereome and of secondary canals has to be mentioned. That stereome which appears in connection with primary tissues only may properly be spoken of as primary. Of this there are but two slender bundles (plate 23, fig. 6), which consist each of a few (less than a dozen) slender, very thick-walled elements buried in a mass of material derived from the primary leptome by the swelling of the cell-walls till the lumina become indistinguishable.

The method of origin of these sclerenchyma cells is difficult to determine, and will be discussed beyond.

The pericambium appears to be continuous, but so far as I am aware the formation of stereome does not involve the cells of this layer. The configuration of the cells of the adjacent secondary cortex is at this time (a root 2 mm. in diameter) very curious, the walls having been distorted, as if by stretching in a radial direction from the primary sclerenchyma as a center. This result would seem, however, to be due to compression by

the growth of a mass of secondary stereome which arises within the primary stereome and is removed from it, in a root of 2 mm. diameter (plate 23, fig. 6), by about 35 microns toward the center.

This secondary stereome strand is larger than the primary strand and becomes an obvious structural feature. For this reason, and on account of its close proximity and its relative position to the primary canals, it may very easily be mistaken for the primary strand. Its cells, however, are larger, and it arises in connection with secondary leptome, and not in relation to the proto-leptome. For this reason its position is more variable than that of the primary strand and may suffer tangential displacement (due to unequal development of the root), as shown in plate 23, fig. 1; and further, for less obvious reasons, the stereome may not occur at all.

Other secondary stereome strands develop, if at all, always in connection with the leptome, as stated for the stem by Fron and François (1901) and by Ross (1908). The particular mode of origin will be discussed later. Each series is circular (plate 23, figs. 1 and 2), as all the members of a series arise normally at the same time, though the series may be more or less discontinuous, owing to unequal development as between the members of the series. In seedlings grown rapidly under irrigation the amount of stereome development is usually notably less than in field seedlings or in others grown slowly.

Secondary resin-canals (plate 22, fig. 13) arise within the secondary leptome in close proximity to the cambium, and in the manner described by Ross for the canals of the stem. They consist at first of two tangential rows of cells scarcely distinguishable from the cambium from which they arose, though quite early they may be recognized by their larger size and the dense protoplasmic contents which at first show by their reactions merely their protoplasmic nature. Ross (1908, p. 260), however, says of these canal-cells: "Die den Kanal auskleidenden Zellen sind durch dichtes Protoplasma ausgezeichnet, das sich mit Chlorzinkiod dunkelbraungelb, mit Alkannin intensiv rot färbt, während sonst das Leptom hauptsächlich stärkereichen Zellinhalt fuhr."

My own observations differ from those of Ross in that the cell contents, when very young, do not react to alkanet as described by him. Very soon after the two cell-rows begin to split away, minute globules of a secretion begin to appear, and these indeed take on the intensive red color of the reagent. This is considerably in advance of the same appearances in the adjacent cortical cells. Preparations treated with alcohol to dissolve out the resin or oil, which might be said to occur, show this very clearly, and further treatment of the same preparations with benzole shows that these intensively staining masses are dissolved out by that agent, and, in the absence of evidence to the contrary, must be regarded as rubber. In the secondary canal-cells, therefore, as in the wall-cells of the primary canals of the root, occurs the earliest appearance of rubber, the secretive activity extending progressively from them to the surrounding tissues, and more rapidly in the primary cortex. It is worthy of especial note that rubber occurs in the wall-cells of canals which normally contain, in the meatus, the resin characteristic of the guayule plant. This point calls for discussion, which will follow later.



The leptome of the root does not show any starch-content in the sieve part, though it occurs apparently erratically in its parenchyma and in the cortical cells adjacent also to the leptome and to the resin-canals. It is also to be found in the endodermal cells close to the primary canals, and occasionally elsewhere, in a 4 mm. diameter root of a field plant.

If, however, we examine a plant grown with an abundance of water, in which the secretion of rubber has taken place only in minute quantities and this in the wall-cells of the resin-canals, an important physiological relation between starch and the secretory canal-cells is indicated. In a root 4 mm. in diameter, which developed in about three months, the distribution of starch and its quantity are very striking. It is present abundantly (a) in a broad, irregular radial band of cortical cells extending from the primary resin-canals, (b) in a narrow and somewhat irregular circular band midway the secondary cortex, and (c) in marked quantities in the cortical cells adjacent to the definitive resin-canals. It is not present in the leptome adjacent to the young resin-canals. It would therefore seem probable that the presence of starch in marked quantities near the resin-canals is related either to the secretion of rubber by the wall-cells especially, or to the secretion of resin. The familiar case of *Pinus*, in which starch occurs near the resin-canals, suggests the latter.

The earliest appearance of rubber, which is secreted by the parenchyma of the cortical rays and of the cortex, aside from the cells of the resin-canals as above noted, is to be seen in the innermost cells of the rays, and synchronously in the outermost cells of the primary cortex, or, if that is absent before secretion begins, of the secondary cortex. This fact is beautifully shown in the tap-root of a seedling from the field, probably less than one year old, collected on July 14, 1908, and measuring 2 mm. in diameter. In this specimen the cells of the primary cortex were completely filled, as also the outer cells of the secondary cortex, there being progressively less and less secretion toward the center of the root. The opposite relation was shown by the parenchyma rays, in the cells of which the amounts of rubber were found to be progressively less and less, as one proceeded from the center outward (plate 23, figs. 3, 7; plate 40, figs. 2 to 4). In a still younger seedling, perhaps three months old, about 1.2 mm. in diameter, rubber is to be seen only in the cortical cells adjacent to the primary canals and in the few innermost cells of the cortical rays. The amount is so small here that, while it may readily be seen with the eye, the photograph does not differentiate it.

## HYPOCOTYL.

### PRIMARY STRUCTURE.

The primary cortex consists of six layers of cells, including the endodermis. The epidermis becomes rather strongly cuticularized and many of the cells are papillate, or, more correctly speaking, form short, round-ended trichomes, which are usually one-celled, though two-celled trichomes are found in a few instances (plate 23, fig. 9). The angles of the cortical cells adjacent to the inner faces of the epidermal cells are collenchymatized, but in deeper layers this character is not present. Chloro-

plasts, few in number, however, are present in the cortical cells. The endodermis is well marked and contains a good many large starch grains. The Casparian spots are readily recognized.

The stele (0.18 mm. in diameter in a hypocotyl 0.53 mm. in diameter) is, at an early age, tetrarch above the zone of transition to the root. The four bundles are received into the hypocotyl in pairs, one pair from each cotyledon, in which they constitute the median trace. After reaching the lower part of the lamina they unite, as they do in the lower part of the hypocotyl (in the "collet"), to form a single bundle.

In addition to the median paired cotyledonary traces, there are delivered into the hypocotyl four lateral traces which meet in pairs to constitute two bundles which pass inward and downward. Each takes a position, the one on one side of the stele, the other on the other, in a vertical plane at right angles to that which divides both cotyledons. They are the "faisceaux latéraux" of Dangeard (1889, p. 85). So far, then, this plant satisfies the "cas secondaire" of his root type with two bundles, found in the Compositæ and certain Ranunculaceæ. According to Dangeard, however, the behavior of these bundles is, to use his own words, as follows: "Les premiers (f. médian) se comportent comme dans le cas général;<sup>1</sup> les latéraux s'anastomosent plus ou moins longuement avant de rejoindre le médian vers le bas."

If I interpret Dangeard's statement correctly, we should find that the lateral traces (plate 24, figs. 2 to 5, 12) anastomose with the median. This, however, I do not believe to be the case. By following the figures it will be seen that the lateral traces are to be seen in the upper part of the hypocotyl, but end rather soon. The broad medullary ray between the pairs of median bundles is then unoccupied, and remains so till the cauline bundles encroach upon it. Between these cauline bundles, at the proper level, the slender end of the lateral cotyledonary trace may be seen, quite single and separate from them (plate 25, fig. 10). In the diagram (plate 24, fig. 13) the fused lateral traces are represented as being much shorter than in that given by Dangeard for *Catananche lutea*.

In types with a tetrarch root-structure this trace passes downward and articulates directly with two of the primary hadrome strands. This, e.g., occurs in *Caulophyllum thalictroides* (Butters, 1909) and in numerous other plants cited by Dangeard (*l.c.*).

The intervals between the lateral and median bundles are occupied by two cauline traces, or, more properly speaking, by one (lateral prophyllary) and a half (of the corresponding median prophyllary) traces. There thus appear in the higher levels of the hypocotyl:

(1) 8 cotyledonary traces, viz, 2 pairs of half-median traces; 2 pairs of lateral traces.

(2) 8 prophyllary traces, viz, 4 half-traces, a half-trace on each side of the cotyledonary laterals; 4 lateral traces, one on each side of the cotyledonary median pairs.

Passing down, the  $1\frac{1}{2}$  cauline bundles in each cotyledonary median-lateral interval fuse with each other and then with the adjacent median trace. Below the level of this fusion the tetrarch structure is assumed,

<sup>1</sup>That is, as above described.



the paired cotyledonary median bundles becoming somewhat separated. The separation is, I believe, due to the rapid enlargement of the adjacent parenchyma-cells, so that the secondary elements become, in the lower part of the hypocotyl, definitely dissociated, leaving the primary elements occupying the position of the primary hadrome elements of the root. The primary hadrome plate of the root lies, then, in the plane of the cotyledons (Dangeard, *l.c.*, p. 87). In making the approach to the root the leptome masses revolve, two in one direction and two in the other, until they meet, two and two, to form the diametrically opposed leptome masses of the root<sup>1</sup> (plate 24, fig. 2); above, these same leptome masses pass entirely into the cotyledons, with the corresponding hadrome masses, and not into the stem. The continuity of vascular tissues between the stem and root is established secondarily.

The above account of the structure is incomplete in that the presence of an originally single tracheal vessel, extending from within the cotyledon downward through the hypocotyl into the root, has not been pointed out. This trachea (*trachée primitive* of Vuillemin, 1884, p. 183) constitutes a center of development, identical in the hypocotyl and tap-root, for the primary hadrome. It is unnecessary to recount the arrangement of hadrome in these organs, but it is pertinent to insist on the initial centripetal formation of new hadrome elements. The dissociation of the hadrome elements in the hypocotyl—strictly speaking, only in the upper portion—is due, as Vuillemin has stated (1884c, p. 181), to the rapid development of parenchyma, and is analogous to the secondary splitting apart of the wood cylinder in the same organ by the growth of the conjunctiva. In consequence of this interpretation Vuillemin speaks of the paired bundles as “les deux moitiés du faisceau,” which are secondarily separated by “a medullary ray.” The peculiar orientation of the paired bundles represented (but frequently not referred to) by many observers (van Tieghem, Gerard, Dangeard, Goldsmith, Ramaley) is thus, properly I believe, explained.<sup>2</sup>

#### PRIMARY RESIN-CANALS.

These arise in the endodermis, as in the root, as a single canal directly opposite each primary leptome strand (plate 25, figs. 1 to 6). The structure of the canal is similar to that in the root, and consists in its definitive form of eight cells in transverse section. The course of development is not so regular as in the primary-root canals, the meatus being ultimately more cylindrical. Not infrequently the earlier divisions do not all take place, so that three instead of four cells line the meatus (plate 25, fig. 2). As these canals pass into the root they pair off, each pair coming to occupy the position already described, namely, opposite each of the two primary leptome bundles. When more than two canals are encountered in this position it is the result of branching. Occasionally both branch either once, or frequently twice, giving rise at length to four or even six canals, though more frequently three or four only occur.

<sup>1</sup> The above account may be applied to *Parthenium incanum*, *Lactuca*, and *Helianthus* in its main outlines, and is a type, I believe, of wider applicability than usually supposed.

<sup>2</sup> As for the rest of Vuillemin's views, regarding the nature of the hypocotyl and cotyledons, I will say only that they appear to me somewhat strained, and far less in accord with the course of development than those of Dangeard (1889).



## STEREOME.

The primary stereome arises early in the hypocotyl, as four slender bundles just within the canals, within the outermost part of the primary leptome strands. Occasionally, also, endodermal cells adjacent to the canal may undergo sclerosis, both in the hypocotyl, stem, and leaf (plate 25, figs. 5, 6, 11).

That unmodified pericycle cells lying just within the endodermis and opposite the leptome become sclerosed seems possible (plate 25, fig. 6), but doubtful. I find that the pericycle is quite frequently interrupted (plate 22, fig. 12), in which event the stereome must arise in the primary leptome. Its further development is contributed to chiefly by elongated elements in the leptome, and a few elements are sometimes derived also from the leptome parenchyma. Nearly all the elements (except those of parenchymatous origin) which play this part enlarge greatly (plate 25, fig. 4) and cause marked displacement in the surrounding tissues. Vuillemin (1884a) has described stereome arising, in the Compositæ, in the secondary, but not in the primary leptome, in *Achillea*, *Artemisia*, *Anthemis*, and *Leontopodium*. From my own studies I am forced to the conclusion that this takes place in the primary leptome.

## SECONDARY STRUCTURE.

The prophyllary bundles, above referred to, arise in the intervals between the cotyledonary bundles, *before* the establishment of interfascicular cambium (plate 24, figs. 2 to 5, 12). This, when complete, incloses the cotyledonary hadrome, and there is thus established the basis for the imposition, on the primary stele, of secondary, true stem topography. It may be pointed out, however, that the cambium does not lay down secondary hadrome in all cases in immediate contact with the primary elements. Thus, in the radii of the median cotyledonary traces (the elements of which do not of course pass beyond the cotyledonary node) secondary hadrome arises which descends from the epicotyl (plate 25, figs. 10 to 10b). Between these there is frequently a hiatus which delimits them readily to the eye, if the secondary changes have not proceeded too far. Nevertheless, though the morphological separateness of the primary and secondary hadrome—and also leptome—is clear, the peculiar topography, the curved outline of the secondary hadrome as seen in transverse section, indicates an as yet entirely unanswered question as to the immediate cause of this. As it is purposed to compare ecological types, further detail will be considered in the following paragraphs.

## FIELD PLANTS.

The pith in a specimen about 1.8 mm. in diameter displays at an appropriate level two gaps (plate 25, fig. 7), each in the position of a primary medullary ray, containing the primary bundles<sup>1</sup> constituting the lateral leaf-traces, while its transverse outline still reflects the vascular topography of the primary condition. Surrounding the pith is a closed compact column of hadrome which is broken up radially into broad wedges

<sup>1</sup> These undergo little or no secondary thickening, except in a restricted region below the cotyledonary collar.

by secondary parenchyma rays (plate 25, fig. 7). The primary rays are for the most part entirely closed, though two of these are suggested by the topography of the pith, as above indicated. No more resin-canals have appeared. The primary stereome bundles have extended inward by the transformation of the primary leptome, and the primary resin-canals are still present. Small secondary stereome strands are present on the outside of several other bundles, as indicated in plate 25, fig. 10. The endodermis is recognizable by its starch-content. The primary cortex is much reduced, its tissue having been sacrificed to the development of a thick cork, the original peridermal divisions of which take place in the outermost cortical layer of cells (plate 23, fig. 8).

The seedling in question (plate 25, fig. 7) was less than a year old, probably four to six months. The epicotyl was 8 mm. long, with a few small leaves, and was collected on July 24, 1908.

An etiolated seedling (plate 25, fig. 9) of the same diameter, with an epicotyl 2 cm. long and about three months old, shows a similar topography, save quantitatively. There is a weaker and more irregular development both of hadrome and of leptome. There is no additional stereome beyond the four primary strands. The primary cortex is thicker and the cork thinner. This seedling was supplied with abundant water and the shade of a muslin cloth, with the effect of producing responses correlated with a relative reduction of transpiration and to loss of water from the surface of the stem. The greater leaf-area, together with a more slender axis, results, however, in a greater transpiration stream relative to the diameter of the wood cylinder, with histological results to be noted beyond.

An irrigated plant (plate 25, fig. 8) of slow growth, one which was plentifully supplied with water, exposed to full illumination, but limited in the spread of its roots, is very instructive in this connection. Under these conditions we must assume a strong transpiration stream, at least stronger materially than is usually the case in field plants. The specimen had a diameter of 2.5 mm. and was not more than three months old, and on this account alone was therefore a trifle larger and more advanced in development than the preceding. In its cork development it resembles the field plant, and has suffered the same reduction of the primary cortex. In fact, in both cases one of the primary canals is just cut out by the periderm. The deeper medullary rays communicate with the pith, indicating secondary enlargement of the latter. The amount of wood as compared with the field plant is much greater relative to age, but somewhat less relative to radial measurement, and there is a relatively larger growth of the secondary cortex. Most remarkable is the large and irregular development of stereome. This irregularity is constantly associated with a plentiful water-supply and is an expression of a general tangential displacement of cortical tissues, as revealed by the later positions taken by the primary resin-canals and the obliquity of the leptome masses, the position of which predetermines that of the secondary stereome.

Aside from the total quantity of hadrome, these three ecological types present histological peculiarities which are related to the transpiration stream. The number and size of the vessels in the field plant (plate 26, fig. 2) are scarcely inferior to those in the irrigated plants (plate 26,



fig. 4), while the etiolated plant (plate 26, fig. 3) has vessels somewhat fewer, but of more uniform size and notably larger. The mechanical elements of the wood are thicker-walled and somewhat smaller in the field plant (plate 26, fig. 5), and are nearly isodiametric. They are of much the same character in the other two, except that they appear more compressed tangentially, especially in the irrigated plant (plate 26, figs. 6, 7).

The stereome also presents differences which are still more striking, aside from the relative amounts already spoken of. In the field (plate 26, fig. 8) and etiolated (plate 26, fig. 9) plants the cells are closely set together, but are smaller on the whole, and in the field plant have smaller lumina. In the irrigated plant (plate 26, fig. 10) the shape and size vary greatly, the lumina are very small, and the intercellular material is much more extensive. The whole appearance leads to the impression that there is a good deal of distortion during development, so that the fibers are pushed about and disarranged, the tissue becoming less compact. If my view of the origin of the stereome is correct, the explanation of this condition may lie in a less complete transformation of the sieve-tissue into stereome. The collapse of the unsclerified cells would cause displacement, and the irregularities due to change in position and unequal growth of the stereomatic cells would ensue. The more slowly growing tissues are the more regular and the more compact. The stronger development of mechanical elements in irrigated plants, both in the cortex and stele, appears to be correlated with the larger growth of shoot, while the larger vessels of the etiolated plant indicate the greater proportion of transpiring surface (the leaf-surface) to the diameter of the stem.

#### LATER SECONDARY STRUCTURE.

As the hypocotyl approaches a diameter of 3 mm. a total movement outward of the whole vascular system (including the entire wood cylinder) takes place, a result of the enlargement of the pith and adjacent parenchyma-rays tissue (plate 26, fig. 1; plate 28, fig. 3). The inner edges of the hadrome plates or wedges become more or less bent, because their edges are held together unequally by the original solid mass of early secondary hadrome, which splits usually in four places, corresponding apparently with the primary parenchyma rays. These, therefore, are at first closed and later opened secondarily, as shown in the figure (plate 25, fig. 8), in which the rupture of the xylem cylinder is beginning. In a field plant this expansion of the pith is also accompanied by a considerable tangential growth of the medullary rays. This circumstance, together with the relatively slower rate of growth of wood, brings about the result that in field plants (plate 25, fig. 7) the amount of wood is relatively less than in irrigated plants (plate 25, fig. 8), and the medullary rays are wider. The thickening of the parenchyma rays is shown most strikingly in an etiolated seedling, the consequent rupture of the wood<sup>1</sup> in which is shown in plate 26, fig. 1.

As to the cortex, the growth has continued in all of its parts in such a manner as to still keep the primary cortical canals included within the

<sup>1</sup> The separation of the young hadrome in succulent roots in this manner is well known.



living part. Two series of secondary canals have arisen in the hypocotyl of the size under consideration, whether the growth has been rapid or slow under irrigation (plate 29, figs. 3, 4), or slow in the field (plate 28, fig. 3); but the total number of canals is greater in the irrigated plants, as would be expected in view of the more numerous wood plates. The radial depth of the cork has not increased in any appreciable amount in the field plant, but is more uniform than in a rapidly growing plant, in which it is relatively much thinner (plate 29, fig. 3).

It is of interest to extend our comparison to rapidly and slowly growing irrigated plants. The chief point of difference is seen in the much greater tangential development of sieve-tissue, and, later, of stereome, relatively to the size of the plant in slowly growing specimens (plate 29, fig. 4). This statement may be extended also to the mechanical elements of the wood, in which the libriform cells are of smaller diameter, have smaller lumina and are more cylindrical, implying a greater amount of intercellular cementing substances. The vessels too are of smaller diameter, and, though this is compensated for by their greater numbers, the capacity of the vessels in the more rapidly grown plant is considerably greater (plate 27, figs. 6, 7). The phloem presents analogous differences, having in the slowly growing plant a structure denser and much more extended tangentially than in the rapidly grown plant, and in this, as in the character of the wood, resembling more closely the field plant (plate 28, fig. 3). A still further difference, of more fundamental character morphologically, is the development, in slowly growing irrigated plants, of stereids in the pith (plate 29, fig. 4). So far as I have been able to observe, the stereids occur under no other condition in the hypocotyl, though, as will be shown, it occurs normally in the pith in the definitive stem (plate 29, figs. 5, 6).

The observations on the structure of the wood in the seedlings studied, regarding especially the water-carrying elements, are of peculiar interest as they stand in relation to those of Cannon (1905), who studied comparatively irrigated and non-irrigated desert woody plants of eight species. His general conclusions, undoubtedly supported by his observations, are that "there can be no mistaking the fact that branches of irrigated plants (even if semi-irrigated only) are poorer in conductive tissue than branches of the same diameter of non-irrigated plants," but he says at the same time that this "is an unexpected condition." Further, "irrigated plants organize each year a larger amount of wood—which contains a relatively large amount of non-conductive tissue—so that it happens that non-irrigated and older stems have more vessels than irrigated and younger" of the same diameter.

For the reason that I found, to my surprise also, that some of my observations coincide with Cannon's, I venture to cite certain concrete instances, and state these, together with those already presented, in brief fashion, by way of instituting a comparison of our results:

1. In field plants (the seedlings above studied) the vessels are as large as in irrigated plants of slow growth, or larger, and are slightly more numerous. The stems are of nearly equal diameter (plate 26, figs. 2, 4; plate 27, figs. 6, 8).

2. On the contrary, in irrigated seedlings of very rapid growth the vessels are much larger, though not quite so numerous, as in the plants mentioned under (1); but the total amount of wood is considerably greater relative to the diameter of the stem (plate 27, fig. 7).

3. The terminal twig of a field plant of very large size, in which the amount of growth in any twig was very small in one season, is contrasted with an irrigated twig of rapid growth. The wood cylinders are equal in diameter; the vessels are somewhat larger in the secondary xylem of the field plant. But in the protohadrome the vessels are larger in the irrigated plant (plate 27, figs. 4, 5). Both twigs of the same and last season's growth.

4. Two twigs of about the same diameter of wood cylinder, one a field twig two years old, the other irrigated, one year old. The total number of vessels is greater in the field plant, and there are more large and more smaller vessels. In the protohadrome, however, the reverse as regards size is true. But the number of vessels in either year's hadrome in the field plant is probably the same as, or is less than, that in the irrigated plant (plate 27, figs. 9, 10).

5. On the contrary, in another irrigated stem 6.5 mm. in diameter, the number and size of the vessels are enormously superior to the number and size in a field plant (plate 27, figs. 2, 3).

6. The protohadrome in a field seedling of usual growth compared with that of an irrigated plant, before secondary xylem has appeared in either case. In the irrigated plant, in which growth is rapid, the elements in question are much larger (plate 26, figs. 11, 13).

7. The protohadrome in a peduncle, through which there is, relative to its size, it can hardly be doubted, a very large transpiration stream, is composed of very large elements (plate 26, fig. 12).

8. In an etiolated seedling (plate 26, fig. 3), in which the size of the stem remains small in relation to the total transpiring area, the size of the conducting elements is greater, and their numbers scarcely less, than in a field or irrigated seedling of approximately the same size of stem.

9. In the tap-root of very rapidly grown seedlings the vessels are much larger and the amount of mechanical tissue much less.

These observations are in part antagonistic, in appearance at any rate, to those of Cannon, and in part agree with them. They must therefore be harmonized among themselves as well as with Cannon's. In attempting to cover all the cases with one explanation, we must not forget that the problem indicated is a complex one, inasmuch as the ratios of mechanical tissues in the two types enter into it. It will, however, suffice to speak of the conducting elements alone at the present moment.

In stems of guayule of a given diameter in field and irrigated plants, the amount of wood is greater in the latter. In wood cylinders<sup>1</sup> of equal diameter the same holds true. This is due to (a) the smaller amount of cortex in irrigated plants and (b) the narrower medullary rays. We may assume that the growth in thickness of the stem is correlated with the growth of the shoot above. In the same period, the total amount of con-

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<sup>1</sup> Wood, medullary rays, and pith taken as a whole.

ducting tissue formed in irrigated wood is undoubtedly much greater than in that of field plants, but the amount of mechanical tissue is also greater. Putting these facts together, it seems reasonable to conclude that the *capacity of the conducting elements is correlated with the maximum transpiration stream*. The relative numbers, and therefore their size, depend primarily upon other conditions productive of the development of mechanical elements. On comparing the shoots of field and irrigated plants, it is clear that the mechanical conditions in the latter are those under which mechanical tissue would be developed. The mere weight of the foliage alone would be expected to insure such responses.

#### ADVANCED SECONDARY CONDITION OF THE HYPOCOTYL.

In a more advanced stage of growth nothing of especial note, beyond that already pointed out, presents itself for discussion. One point, however, is worth noting, namely, that the daughter and granddaughter cells of the cortex remain arranged in tetrads chiefly, thus giving the whole tissue the appearance of consisting of pairs and tetrads of cells. The original, but enlarged, intercellular spaces are very much in evidence (plate 28, fig. 4). Regularly shaped and disposed spaces, such as have been described for the root, do not occur in the stem.

#### AGE AND STRUCTURE IN THE SEEDLING.

Both popular and scientific discussion frequently turn on the correlation of age and structure in the guayule. Inasmuch as the hypocotyl is the oldest portion of the stem, it is worth while to indicate the structure of field plants of known age. A seedling from Station 2, which was less than one year old when collected in April 1909, with a stem 5 cm. long and 4.6 mm. in diameter at the base, shows in the hypocotyl the structure represented in plate 30, fig. 1. The living cortex (primary) is very sharply delimited from the cork on account of the rubber-content of the living cells. It will be seen that the specimen closely resembles the slowly grown irrigated plant above described, while in point of fact it is a plant of rapid growth for field conditions, being much above the average size for the locality in which it was collected. It is seen from this, what will in any event be understood, that all field plants are not alike, the water-supply varying at different times in different habitats, thus inducing at times growth quite similar to that which usually occurs under more favorable conditions. This seedling has, in addition to the four primary canals, three series of secondary canals. One below the average size, of the same age, with an epicotyl 8 mm. long, 2.4 mm. in diameter, has only the four primary canals. These are finally thrown out when a diameter of 6 to 7 mm. is attained, and therewith the whole of the primary cortex is lost.

In a seedling of the same diameter three years old, it is possible to see three annual rings of wood, marked by the larger pores of the first growth of each season. There are in the same stem, aside from the four primary canals, three series of resin-canals, one in the primary and two in the secondary cortex, so that there are marks of three zones of cortex, the primary and two secondary, corresponding apparently with the three



seasons of growth. Comparing the two cases, we find that the structure attained in the cortex by a seedling of one season may be the same as that attained in three years by one of slower growth, while the number of growth-periods is reflected, albeit frequently only indistinctly, by the wood. It is, however, generally true that the ring-structure may be made out.

### EPICOTYL.

Seedlings partially etiolated by being grown under a muslin screen, in which the internodes have lengthened, render the analysis of the tissues easier. The lowermost internodes of such seedlings receive primarily six bundles (plate 24, fig. 5) from the hypocotyl, but the number is at once increased, so that immediately above the base eight or even more bundles may be counted (plate 24, fig. 6). The increase is more marked in plants with short internodes, and the primary condition is quickly masked. The development of the stereome which arises in the primary leptome is in the primary numerical relation, there being at first six bundles, opposite the median and lateral leaf-traces of the first two foliage leaves. These relations are shown very beautifully in a section taken from a seedling which had developed one-sidedly, and this is figured in plate 30, fig. 2. The relations of the primary cortical canals received from the hypocotyl are well shown also in this section. One pair of these accompanies the median leaf-trace of the first leaf, the other pair that of the second leaf. The third petiole may receive two or one, and this is true of all the earlier leaves as far as the tenth node, approximately. The primary condition, that in which two lateral canals occur, may recur even in later stages of development, but only infrequently. As they pass into the leaf one becomes smaller and ends blindly (plate 38, figs. 3 to 9), while the other extends into the leaf-blade. In this there is a striking similarity between the earlier foliage leaves and the cotyledons, constituting a morphological argument against the theory that the cotyledons are not primitively leaves. The absence of medullary<sup>1</sup> stereome, mentioned above in the paragraphs dealing with the hypocotyl, will be noted, and this condition, as in the case of retoños, persists until the level of the tenth internode or thereabout. Sections of field seedlings with short internodes at a distance of several millimeters from the insertion of the cotyledons show no medullary stereome, and this is true also of medullary canals.

The same section (plate 30, figs. 3, 4) serves, in addition, to show very clearly the origin of the periderm, which in the definitive stem, as in the earlier internodes, occurs in the first or outermost cortical layer of cells (as shown by Ross, 1908). Fron and François (1901) state differently, and their drawing depicts the earliest suberogenous divisions in the second layer of cells; in this, however, they are in error. Their drawing is taken from a section through the base of a petiole, as the position of the leaf-traces, so labeled, shows. In such a section, it is true, the earlier divisions will be seen in the second, third, or even fourth layer. I have introduced two figures taken from portions of the tissue in question on

<sup>1</sup> I use this in a purely descriptive sense. "Perimedullary stereome" has been used. The origin of this stereome is dealt with beyond (p. 110).

opposite sides of the same section. In the position opposite the first leaf-trace the divisions occur in the second layer; at the other end of the diameter, in the outermost. The periderm figured by Fron and François is therefore the leaf absciss layer. Leaf fall in the guayule is consummated only slowly, and, as compared with more familiar examples of the temperate regions, is imperfect in its time relations. The layer is not sharply defined, and the disintegration of the tissue is irregular, the result of the uneven and irregular character of the component cells of the absciss layer.

The epidermis, both of stem and leaves, in the epicotyl is clothed with a single type of trichome found throughout (plate 30, figs. 5 to 11). There are two derived kinds, a T-shaped hair predominating, with a few scattered hairs of a type seen in *Chrysoma* (Lloyd, 1901) and in other Compositæ, viz, the whip-hair, but in which, in the guayule, the terminal cell remains undeveloped. The trichome does not, therefore, become flagellate, as in the related species, the mariola (*Parthenium incanum*), and in many Compositæ (Vesque, 1885). In certain places, as in the axils of the leaves, floral bracts, and corolla, transition forms may be met with, indicating that the two kinds have been derived phylogenetically from a single type. The fact that both are present in different Compositæ, but in different ratios, may be used to support the view that the trichome clothing is a character which has been brought about by gradual change and not by the sudden dropping out of one or the other kind. The T-shaped hairs clothe the plant very completely and smoothly, the terminal cells all lying very nearly parallel to each other, and to the axis, on the various organs. The density of the covering varies, however, with the size of the organ, as the individual hairs show no substantial amount of response to varying external conditions.<sup>1</sup>

Before leaving this part of the subject it is necessary to point out that in seedlings in which the stem elongates slowly, as in the field, the primary cortical canals of the hypocotyl behave in a manner which has not been observed in etiolated plants. The two pairs, associated with the median leaf-traces of the two early foliage leaves, instead of passing directly into the petioles, anastomose and then, from the transverse lacuna thus formed, canals pass off to enter the leaves. Other canals have been noted to rise from the lacuna and to pass up into the epicotyl; a reanastomosis within a short distance has been observed (plate 36, figs. 7, 8). A section of a field seedling made through the cotyledonary node, or at any level, if the internodes are undeveloped, will almost invariably show widely spreading divarication of one or more of the canals (plate 36, fig. 6). In a word, the canals constitute a branching system, each more or less in communication with the other.

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<sup>1</sup> The mechanical conditions in axils of leaves and in the capitula cause superficial changes in the shapes of the trichomes.

## THE DEFINITIVE STEM.

## PRIMARY STRUCTURE.

After the tenth internode, approximately, has been laid down, the stem takes on its definitive structure. The number and appearance of the various structures within the growing tip vary a good deal, according to the rate of growth. This is largely due to the crowding together of the nodal characters, but in part also to the size of the terminal bud, and therefore to the number of leaves. In a thick apex more bundles of primary elements appear at a given level (plate 31, fig. 3); also the size and frequency of branching of the canals is greater within a given zone (plate 36, fig. 5). For the purpose of description it will serve to present briefly the differences observed, at various levels of a stem one year old, of normal growth-rate in the field, as this will give an epitome of the development of the tissues. The specimen before me is a twig which grew in 1908, collected at the close of its elongation for that season. It is 11 cm. long, 4 mm. in diameter at the base, and 1.6 mm. just behind the tip. The structure at the levels mentioned is as follows:

Within the last millimeter of the tip one finds the vascular tissues undifferentiated, though the medulla and vascular zone are recognizable. The primary cortical canals appear opposite median leaf-traces,<sup>1</sup> but nowhere else (plate 38, fig. 1; plate 31, fig. 5). The starch sheath (endodermis) is recognizable only by the starch-content, which appears only opposite leaf-traces, while starch is absent from the endodermis elsewhere. Within half a millimeter further down, at a diameter of a millimeter, all the 5 medullary canals appear, 17 vascular bundles are distinct, and 16 cortical canals are present (plate 31, fig. 4). In perhaps half of the bundles spiral vessels have developed. These are in curved plates of 1 to 3 vessels, each separated by wood-parenchyma. The epidermis is densely clothed with T-shaped trichomes. The endodermis may be traced completely around the stele, on account of its starch. At this level may be seen the earliest indications of the stereome bundles in the primary leptome and in the pith.

At 10 mm. from the apex (diameter 2.5 mm.) the collenchyma of 4 to 6 rows is well developed. The characteristic thickening is first seen in the periclinal walls, and these become still more conspicuously thickened in the later stages. The larger bundles have xylem plates 6 to 8 cells deep radially. Interfascicular cambium is being developed. The stereome is still thin-walled, but the definitive size of the cells has been reached, and thickening has taken place at the angles. In the section before me I count 25 primary cortical canals and 10 medullary canals. The section was evidently taken just above the plane in which the pith-canals branched, as two of the canals are cut at the fork.

At 15 mm. (diameter 3 mm.) mechanical elements have appeared in the hadrome, and the stereome is more advanced as to the thickening of the walls. The collenchyma has been somewhat stretched periclinally, the walls so placed being much thicker. The walls of both cortical and

<sup>1</sup> Very occasionally a pair, a single one on each side of the trace, occurs.



pith cells have thickened, and in the walls of contact the reticulations, due to the broad, ovate, closely-set pits, are very noticeable. The interspaces are large.

At various lower levels, depending on the time of the year in which the material is taken, will be encountered the young periderm. Ross<sup>1</sup> speaks of this as beginning very early, and in his material as reaching close to the apex. If a newly grown twig is examined toward the close of the season it will be found that the periderm embraces only a lower zone (of a thickness depending on the rate of growth) at the base of the stem, and its growth involves casting off the leaves which remained on the upper portion of the twig of the previous year. This uppermost zone, carrying the overwintered leaves, undergoes some growth with considerable lengthening of the internodes, so that the leaf-scars of the winter bud do not crowd each other as do the bud-scale scars in plants of the temperate regions. The periderm passes upward from this zone, and during the following dry season slowly cuts away the leaves, until by midwinter, earlier or later according to the character of the season, all the leaves of the previous growing season, save the terminal ones, are cast off (plate 14, fig. B). As the periderm extends toward the apex of the twig the epidermis is fissured concurrently, beginning at the base.

A section near the base of the season's growth shows the following structure: The periderm is three to four cells deep, measuring 0.1 mm. The xylem bundles measure about 0.5 mm. on the radius, and the pith has a diameter of 1 mm. Nearly all the bundles are supplied with both cortical and medullary stereome. Tracheids are fewer in the outermost zones of the xylem. The primary cortical canals and pith canals have generally enlarged, the largest measuring 0.3 to 0.4 mm. tangentially, with a radial diameter of 0.15 to 0.2 mm. This section has one completed series of secondary cortical canals, and a second row begun. The epidermis is slightly fissured. This amount of growth and secondary change is by no means the maximum possible. The thickest part of the stem of one season's growth of the seedling shown in plate 46, fig. A, had five series of secondary canals, and cork 0.5 mm. thick, the depth of the cortical tissues, primary and secondary, being 2.5 mm.

A stem of two growth-periods shows the primary and one series of secondary canals, but the two seasons' accretions of wood are reflected in the annular structure of the wood, as in the seedling hypocotyl before mentioned. Here also, therefore, the relation of structure to age is less apparent in the cortex than in the wood cylinder. The whole of the outer leptome (that embraced between the primary and secondary series of canals), is stereomatic; that within the secondary series still retains its sieve character. A considerable thickness of cork has developed.

Later changes need not be followed year by year, and it will suffice to point out the more important features summarily. The inner periderm normally does not begin until the stem attains a diameter of over 10 mm. (Ross, *l. c.*), and the primary cortical canals may still be found up to this time or even very much later, *e.g.*, in a stem 28 mm. in diameter, with cortex, including bark, 5 mm. thick. The penetration of the inner periderm

<sup>1</sup> His material appears to have been collected in December.

is not a clean-cut process, such as we see in our common trees and shrubs, but first appears directly opposite either a primary stereome bundle or a primary canal, as an ingrowth, simulating invagination (plate 32, fig. 4). The absciss layer which effects leaf-fall is similarly clumsy, so to speak. This tissue consists of a quite irregular layer of cork-cells, continuous with the primary phellogen. The outermost cells, those, namely, immediately beneath the base of the leaf, first become suberized.

Until an advanced age is attained, the inner periderm does not cut deeply. In old stems, 20 to 50 years of age, light-colored layers of cork may be seen penetrating to half the depth of the cortical tissues, but quite irregularly. It is of interest to note here that this cork presents a special practical difficulty in the factory in handling the comminuted shrub after it has passed through the pebble-mill. The bagasse is then, with the exception of this cork, which has been broken up into flakes, separated in water, the rubber and the cork flakes floating and the remainder sinking. Only by means of pressure under water or prolonged soaking may the cork be waterlogged, when it sinks, leaving the clean rubber still floating. These layers of cork are seen in plate 2, fig. B, from a photograph of a stem certainly forty years old.

#### SECONDARY STRUCTURE.

The secondary cortex is characterized by alternating concentric rows of stereome bundles and resin-canals. Between succeeding stereome mass and leptome parenchyma (canal-cells, consisting of endothelium and usually a single subjacent or supporting layer), there frequently intervenes no tissue at all, and the stereome occupies the whole of the space between adjacent resin-canals. In the inner part of the secondary cortex one finds alternating canals and "soft" leptome, the composition of which raises some points of question. The canals, as described correctly by Ross (1908), arise as a double row of cells derived directly from the cambium (plate 22, fig. 13). Surrounding the "secreting" cells is at least one layer of leptome parenchyma, the usual condition in slowly growing plants. In irrigated plants there may be two or three (or occasionally more) layers (plate 29, fig. 1). This is followed, radially, by a mass of sieve-tissue (plate 32, fig. 2), which may be regular in transverse outline, and completely uninterrupted by parenchyma until another canal is laid down, or it may be narrow and more or less irregular, as in irrigated plants (plate 25, fig. 8; plate 29, fig. 4). In any event, the sieve-tissue occupies the radially placed space, broadly speaking, between successive canals, and *it is in this space that we find stereome later.*

The manner in which the stereome arises is, in broad outline, as follows: The outermost (on the radius) leptome cells undergo transverse enlargement and become stereomatic. Successively other adjacent cells lying farther in behave similarly. The resulting tissue, however, occupies more space than did the original cells from which it arose. As the total space which is occupied by the stereome is usually identical with the total leptome, it follows that there must be some readjustment. This is brought about by the discontinuous sclerosis of the leptome, so that irregularly alternating masses of this are destroyed and become compressed.



The stereome develops, therefore, within the leptome,<sup>1</sup> and in its definitive form a portion of the leptome comes to occupy the volume of the whole. The definitive stereome may be flanked more or less completely by sclerosed leptome parenchyma, and even the adjacent cortical cells, especially in the peduncle, may take on this character.

With reference to origin, in general terms, I am at variance with Ross, who says on this point: "Durch die Tätigkeit des Kambiums entstehen abwechselnde Gruppen von zartwandigen Elementen und von Sclerenchymfasern. In der jüngsten Gruppe der letzteren geht die Verdickung der Zellwände erst sehr allmählich vor sich, und in den zartwandigen Schichten zwischen dieser und dem Kambium kommt der Secretkanal zur Ausbildung." I believe that I am not unduly criticizing Ross's statement by saying that it is misleading. It would seem more consonant with the facts to say that through the activity of the cambium alternating groups of leptome parenchyma and prosenchyma arise, and that the stereome arises within the latter. The resin-canals arise from two adjacent tangential layers of the thin-walled parenchyma.

The change of any particular cells into stereome is not complete before the end of the third season's growth, as nearly as we may judge. This secondary occupation of the leptome by the stereome is particularly well shown in a preparation made of the cortex of an old stem (plate 32, fig. 2). The sections were treated with xylol so as to extract the rubber, leaving the tissues empty and distinct. The stereome was seen to occupy, with few exceptions, all the space previously occupied by the sieve-tissue.

#### ORIGIN OF THE MEDULLARY AND CORTICAL STEREOOME.

Vuillemin, 1884c, p. 223, has described stereome as arising in the pericycle in the *Compositæ*, but he does not show its precise origin nor that of its constituent elements; nor does his description of the leptome (*l.c.*, p. 99) fit the conditions found in *Parthenium argentatum*. According to Vuillemin, the sieve-tubes are of much larger transverse diameter than the companion cells, and this is not true of our plant. There are, however, broad elements with oblique end-walls,<sup>2</sup> intermixed with sieve-tubes and companion-cells to form a mélange in which the sieve elements are generally in contact with each other throughout the whole leptome mass, and do not usually form isolated islands, as generally described for the *Compositæ*. These elements have common origin in cambium cells; that is to say, the broad elements and the narrow sieve-tissue elements are of common descent. The broad cells, which later are transformed into stereome, do not, therefore, have a distinct origin. The initial division within the mother-cell may be periclinal or radial, separating a broad element, destined to become stereomatic, from a similar one, which again divides once or twice, usually twice, to form the sieve-tissue (plate 31, fig. 9). There is but little difference in the transverse diameter of these, the companion-cells being narrowly fusiform and therefore thickest at the middle, while the reverse, of course, is true of the sieve-cells. The broad elements are recognizable both by their size and by their more tenuous

<sup>1</sup> Vuillemin's description, "sur le dos des faisceaux libériens," does not apply.

<sup>2</sup> The "libriform" of Schwendener, 1874.



protoplasmic content. When they become stereomatic the first step is the great enlargement of their transverse diameters, their walls being thin except at the angles, which are thickened after the fashion of collenchyma (plate 31, fig. 8). During this phase of change the mutual pressure of the developing stereome and the surrounding cortex results in the radial flattening of the latter, and frequently in a crumpling of the walls in the stereome. The limit of the stereome may readily be seen because of the intercellular spaces between the cortical cells and those of the stereome. Meanwhile the sieve-tubes and companion-cells become displaced and, with sclerosis of the stereome elements, are destroyed, and may only with difficulty be observed at all. Sclerosis of the stereome proceeds radially from without inwardly. The compactness of the stereome, as also its regularity and dimensions, depends upon the previous mode of growth of the leptome as a whole, and is therefore more irregular and of uneven texture, in irrigated plants, or, what amounts to the same thing, in rapidly grown plants. Sclerosis also overtakes some of the adjacent leptome parenchyma and, under certain circumstances, some of the neighboring cortical cells, but is not preceded by their enlargement.

The stereome in the medulla (plate 31, figs. 6, 7), which has previously been so referred to for convenience, is, like the above-described leptome-stereome, a constituent of the mestome strand. It arises from elongated elements clustered about the primary hadrome elements, and is the endoxyle of Briquet (1892), but, in the light of the occurrence of bicollateral bundles in the Chicoriaceæ (Vuillemin, 1884a; van Tieghem, 1884), may be susceptible of another interpretation, viz, that it represents the internal leptome in these forms. This explanation is not decreased by the very close analogy between the stereome of the leptome and of the hadrome. In the young condition the tissue which is destined to become stereome is recognizable (plate 31, fig. 6), in transverse section, by the absence of intercellular spaces and the somewhat thickened angles, which, during the stretching of the walls previous to sclerosis, become more apparent, as in the case of the leptome-stereome. Interspaces occur in the adjacent pith and in the hadrome parenchym. The tissue, taking the form of an irregular lunate arc in transverse section, is, therefore, while in contact with the hadrome, not to be referred to this without careful consideration. The progress of change into stereome is identical in all respects with the leptome-stereome, and calls for no particular description; this refers also to the mutual displacement of tissues (plate 31, fig. 7). The analogy to the leptome-stereome is strengthened by the circumstance that longitudinal divisions may take place in the earliest formed elements, before the final complement of stereome cells is arrived at, though it must be said that these divisions are not of sufficiently frequent occurrence to enable one to see more than a very few at a time. The form of the elements further likens them to the analogous ones in the leptome, being elongated and having slightly inclined end-walls. I am therefore inclined to regard the medullary stereome as a tissue *per se* with respect to the hadrome, and as having much in common with the stereome of the leptome, so that it would seem to be properly regarded as representing the internal leptome in genera of the Chicoreaceæ

Precisely these relations occur, to all appearances, in certain of the Boraginaceæ, e.g., *Symphytum tuberosum*, *Nonnea alba*, *Omphalodia linifolia*, etc. (Jodin, 1902). Concerning the leptome, Jodin says, after speaking of the disappearance by crushing of the sieve and companion elements ("les primaires tubes criblés"):

En même temps que s'accroissent les éléments libériens primaires, on peut assister, dans certains genres à un épaississement notable de leurs parois \* \* \* \* Dans d'autres cas, cet épaississement est très faible ou même n'a pas lieu \* \* \* (l.c., p. 308.)

But no such thickening takes place in the secondary leptome. Apparently the thickening of which Jodin speaks goes no further. He does not trace the precise origin of the cells with thickened walls.

As to the medullary stereome, he says little, but his figures show very clearly the earlier, prestereomatic condition which I have shown in my own figure (plate 31, fig. 6). To quote again:

Nous aurons peu de choses à dire de la moelle; nous avons eu occasion de parler, à propos des faisceaux du bois, de la zone pérимédullaire, et des rayons médullaires. La région médullaire proprement dite se distingue par la taille de ses cellules qui sont arrondies en coupe transversale, et qui laissent entre elles de nombreux méats triangulaires. (l. c., p. 322.)

This author, it is seen, points out the same distinctions between the perimedullary zone and pith which I have already made. From this comparison between the guayule and the borages it seems clear that we are dealing with the same behavior, with the very interesting distinction that in the guayule the histological differentiation of the fibers proceeds to completion, while in the plants studied by Jodin they are arrested in their course of development. This appears to be connected with the herbaceous character of the stems in the Boraginaceæ.

In this connection, Schwendener's observations on certain Compositæ are of particular interest:

Im Phloem der grösseren *Aster* und *Solidago* Formen, \* \* \* kommen innerhalb der starken primären Bastbündel kleine secundäre Gruppen mechanischer Zellen zur Entwicklung, welche zum Theil mit den kürzesten Libriformzellen, die überhaupt vorkommen, übereinstimmen, und jedenfalls durchgehend vom typischen Bast verschieden sind. Die Länge diesen Zellen variiert zwischen 150–300 Mik.; die Kürzesten erreichen oft nur bis 80 Mik. Dazu kommt, dass die nebeneinander liegenden schiefen Querwände ähnliche Zick-zacklinien bilden, wie sie sonst nur in kurzcelligen Libriform vorzukommen pflegen. Bei *Aster* bilden sie im Querschnitt netzförmige anastomosirende Bilden, zwischen denen ein parenchymatisches Cambiform stellenweise mit deutlichen Siebrohren, eingebettet liegt.<sup>1</sup>

This distinction made by Schwendener between the sclerosed element of the "phloem" and typical bast applies throughout to *Parthenium argentatum*. This plant, however, differs in the distribution of the sclerosed elements, forming as they do dense masses occupying the space previously occupied by the whole of the leptome and its associated libriform.

Schwendener, however, appears to assume the independent origin of the libriform cells in the leptome, and it is on this point that I advance the view that they have a common origin with the sieve and companion

<sup>1</sup> Schwendener, 1874, p. 152. I have not had access to this paper.



cells. After arriving at this conclusion, I found that Servettaz (1909, p. 232) had already done so with respect to certain of the Eleagnaceæ. The close resemblance in the behavior of the medullary mass of stereome to that of the leptome forces criticism of this view to the effect that the analogy which I have drawn is based on the origin of the stereome in the hadrome and leptome from libriform of an identical mode of origin on either side of the cambium. This view, while admittedly possible, does not agree with my observations, and it is hoped that further research will bring evidence to light which will show which view is correct.

The secondary resin-canals, when fully formed, are composed of an endothelium backed usually by one row of leptome parenchyma (plate 29, figs. 1, 2). In transverse outline, after full development, they are rounded, but gradually become compressed radially as they pass outward toward the bark. The youngest ones measure upward of 0.2 mm. in tangential diameter, and grow in size till, at the outer part of the living cortex, they may measure, in a cortex 5 mm. thick, over a millimeter tangentially, and with a width a third of this. The secreting cells undergo more or less periclinal divisions (with reference to the axis of the canal), producing sometimes two to three layers of cells of endothelial origin. The resin-canals at length frequently become partly or completely closed by an ingrowth of tissue (Lloyd, 1908b) of the same character as the cortex and forming an interesting analogy to tracheal plugs (tyloses). These I call pseudotyloses (plate 32). The cells of the pseudotyloses at length become filled with rubber and continue in a living condition somewhat longer than the surrounding cortical tissue, retaining their normal appearance when the cortical cells toward the outside of the stem have passed over into suber. These parenchymatous plugs are not confined to the very old tissues, but may be found also in young stems and roots,<sup>1</sup> though less frequently. Occasionally the medullary canals, in old plants at any rate, become partially plugged in the same manner (plate 32, fig. 3). In addition to these outgrowths, resembling roughly a bunch of grapes, one frequently finds trichome-like structures, sometimes projecting from the walls and also from the plug-tissue (plate 32, figs. 1, 6). Somewhat similar appearances have been observed by Col, and to this I shall call attention again. In this connection, however, I feel inclined not to agree with this author in his criticism of Vuillemin, who recorded observing structures which he called "poils glanduleux" in the canals in *old* rhizomes of *Arnica montana* (Col, 1903, p. 166). I suspect that these "poils glanduleux" are the same structures as those which I have called pseudotyloses.

The pith undergoes a considerable amount of secondary enlargement, so that in a stem 2.5 cm. in diameter, in which it may still be found in a living condition, its diameter is between 3 and 4 mm. and is irregular in outline. The medullary stereome does not receive any secondary accretion, but the growth of the inner part of the parenchyma rays concomitant with that of the pith, between the edges of the xylem wedges and the flanking stereome, results in the periclinal separation of these. Sometimes one may find that cells near the periphery of the pith have undergone a

<sup>1</sup> I have observed them in the primary canals (plate 32, fig. 7).



rather regularly repeated periclinal division, and the tissue, therefore, has much the appearance of a cambium. It may also happen that repeated divisions occur in a zone about one of the medullary canals. The cause of this is not clear, though it is possible that this also is a mode of growth of the pith (plate 42, fig. 5). It does not appear to be the same as the formation of cork, such as I have observed to occur following injury to the pith or adjacent tissues.

In field plants normally neither pith nor parenchyma rays (save a very few cells) ever become lignified.

The wood in large stems shows the usual distinction of alburnum and duramen. The latter is reddish-brown in color, and all the tracheids are plugged by "Gummipropfen."<sup>1</sup> Temme (1885) and Ross (1908) note their positive reaction to phloroglucin, which I have verified. They are very sharply confined to the duramen in uninjured stems. In one, 2.5 cm. in diameter, in which the plugs are beginning to be formed with irregularity, their genesis may be followed. They first appear as a thin, partial or complete lining, increasing irregularly and gradually filling the lumen. Their conformation suggests the behavior of a dense fluid. Their positive reaction to aniline blue, which is very marked, may indicate that they are at first similar to callus, but, as phloroglucin shows, they later become lignified. In the old wood the plugs appear homogeneous, but they stain unevenly with, e.g., Bismarck brown. Here and there one may note a stratification in planes parallel to the surface of the lumen. That resins are absent from these structures is shown by their total failure to react to alkanet. Molisch (Zimmerman-Humphrey, 1893) showed that gum-plugs behave, with certain reagents, like lignified membranes, but a total parallelism is denied by the above reactions. Lignification in any event would appear to be a secondary feature. Tschirch (1906, p. 1180) identifies the substance as "bassorin."

#### ANNULAR STRUCTURE.

The mature wood shows to the naked eye an annular structure which is frequently regarded as annual-ring structure. In an old stem what is seen in part is a banded appearance due to differences in color intensity (plate 2, fig. B), having no relation at all to a true annular structure, which is readily seen under magnification. This is shown in the two figures, one of which (plate 33, fig. 1) was drawn to scale from the inner alburnum of a very old stem, and the other (plate 33, fig. 2) from one a centimeter in diameter, showing ten rings. It is not at all unlikely that these rings represent ten years' growth, but this would not justify the conclusion that the rings are always correlated with age in years. It must not infrequently be the case that more than two accretions of growth occur in response to the distribution, in time, of the rainfall, and these rings, therefore, represent periods of growth following rain. That these growth-periods for field plants usually coincide with the summer seasons follows from the general

<sup>1</sup> "Wound-gum" (Temme, 1885) seems hardly a suitable term, since the phenomenon is perfectly normal, though, as will appear, the earlier secretion is provoked by natural and by artificial wounding. A direct translation of *Gummipropfen* would be preferable.

character of the precipitation, as elsewhere described. The evidence gives strong support to the view expressed by Holtermann (1907) that the ring-structure of the wood is correlated with cessation and resumption of transpiration. While it is not clear why an annular structure *within* the annual ring is present in the wood of irrigated plants, it is quite possible that it is due to stimulation by successive irrigations. These considerations show that it is practically very difficult to determine the age of a plant by counting the rings, and this is rendered still more so by their short radial measurements. In the case before us (plate 33, fig. 2) 10 rings are counted on a radius of 2 mm., so that the rings, taken altogether, have an average thickness of 0.2 mm. Excluding the innermost (the first season's growth) and the deepest, the rings vary from 0.06 to 0.3 mm. approximately. This, coupled with their frequently great irregularity and indistinctness (Ross, 1908), makes them difficult of recognition.

The suggestion has been indicated inferentially in this connection by Ross that the age of a stem is to be inferred from the number of secondary canals and stratifications of the secondary cortex. A stem examined by him, 19 mm. in diameter, showed eight zones of canals and of alternating phloem layers, and he agrees with Endlich that the stem was about ten years old. I feel quite sure, however, that this inference is far from justified. For example, the stem from which plate 33, fig. 2, was taken was certainly over four years of age, and as certainly eight to ten. There were only *four* rows of secondary canals. In a stem with a radius of 1 cm. I count at least ten cortical zones, while there are but five in another cortex of the same thickness. These, together with the further fact that under irrigation a seedling in five months developed five rows of secondary canals, show that the number of canals depends upon the rate of growth and not upon the number of seasons, and in field plants the number of rows of canals is, roughly, a third to a half less than the age of the stem in years. A cortex 5 mm. thick, exclusive of the cork, taken from a very old plant, about forty years of age, shows about twenty canal zones. Some had of course been cut out by periderm, but scarcely as many as twenty.

TABLE 40.—*Determinations by weight of ratios of bark to wood in field plants*  
(Whittelsey, 1909).

Plant.	Parts of the plant examined.	Ratio of bark to wood.	Plant.	Parts of the plant examined.	Ratio of bark to wood.
I	Roots and thicker stems	$\left\{ \begin{array}{l} 1.1 \\ 1.36 \\ 0.79 \end{array} \right.$	II	Branches and twigs...	$\left\{ \begin{array}{l} 1.29 \\ 1.63 \\ 1.30 \\ 1.7 \\ 1.8 \\ 1.9 \\ 2.1 \end{array} \right.$
II	$\left\{ \begin{array}{l} \text{Roots.....} \\ \text{Trunk.....} \end{array} \right.$	$\left\{ \begin{array}{l} 0.85 \\ 1.13 \end{array} \right.$			

## THE EFFECT OF ABUNDANT WATER UPON ANATOMICAL STRUCTURE.<sup>1</sup>

The effect of irrigation upon the structure of the mature plant is very marked. This is especially noticeable with respect to the relative volumes of the wood cylinder (including pith and medullary rays) and the "bark" (cortex and cork). As this is a question of prime importance economically, it will be treated first.

By means of weighing, Whittelsey (1909) determined that, in various portions of the plant, the trunks are made up of 44 to 65 per cent bark (cortex and cork), the amount of bark being relatively larger in the smaller twigs. The material was quite dry. (Table 40, page 115.)

In Whittelsey's determinations, the pieces examined were first steamed to render it possible to separate the wood from the cortex. A slight

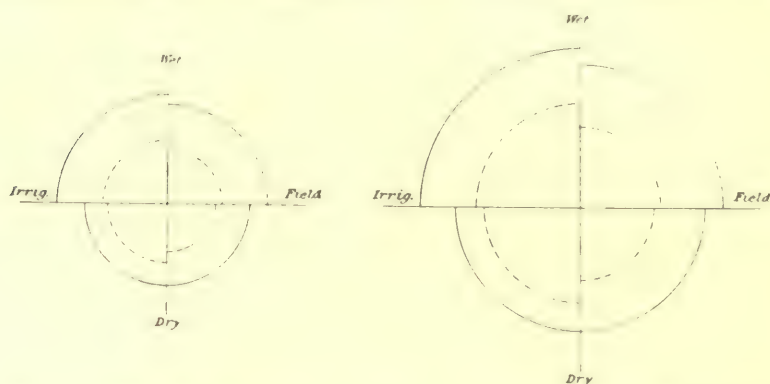


FIG. 16.—Relative dimensions of wood cylinder and cortex, wet and dry, in twigs of field and irrigated plants.  $\times 20$ .

error is introduced by this method, as some of the resin exudes from the cut ends of the cortex and infiltrates into the wood. This error is apparent in table 41, in which the ratios of steamed material are smaller than in

TABLE 41.—Ratio of bark to wood by weight for field and irrigated shrub, as determined after (a) steaming, (b) moist chamber.

Two pieces each of field and irrigated plants (Cedros, April 1909): (a) Field plant pieces 3.9 to 4.8 mm. diameter; (b) irrigated plant pieces, 3.4 to 4 mm. diameter. Each piece of (a) segmented into fourths and alternate fourths placed in each of two lots; (b) segmented into fourteenths, similarly placed in each of two lots. One lot (I) of (a) and of (b) steamed, de-barked, dried in oven, and weighed. The other lot (II) of each placed in a moist chamber till fit for separating wood and bark; then dried in oven and weighed.

Class of plant.	Treatment.	Weight of wood.	Weight of bark.	Ratio.
		gram.	gram.	
(a) I. Field (Cedros) . . . . .	Steamed. . . . .	0.1604	0.2817	1.75 +
(a) II. Field (Cedros) . . . . .	Moist chamber. . . . .	0.1663	0.2968	1.78 +
(b) I. Irrig. (Cedros) . . . . .	Steamed. . . . .	0.311	0.318	1.02
(b) II. Irrig. (Cedros) . . . . .	Moist chamber. . . . .	0.324	0.3608	1.11

<sup>1</sup> The substance of what follows under this caption was presented in a paper entitled "The Responses of the Guayule, *Parthenium argentatum* Gray, to Irrigation," before the Botanical Society of America, at its Boston meeting, December 1909. (Lloyd, 1910b.)



control material softened in a moist chamber. But the small error, less than 1 per cent, is of significance only when such data are used in large calculations.

From the present point of view a volumetric method is of more value than weighing, since the ratios derived by the latter are disturbed by variation in the specific gravity; but as a comparison of the ratios derived by both methods is of use in practice, they have both been introduced. For

similar reasons it is important to know the ratios derived from dry material, and for this purpose the method of displacement of alcohol has been used.

#### RELATIVE VOLUMES OF CORTEX AND WOOD.

The material from which the data tabulated in table 42 were obtained was collected at Cedros.

The irrigated material was taken in September 1908 from stems (fig. 16) of two seasons' growth. The difference in thickness of wet and dry cortex is very slight, and is not given.

It is seen that the volume ratio of bark to wood (when dry) in the irrigated plant is near to unity in the smaller twigs to 0.27 in the larger, up to a diameter of 13.5 mm., beyond which no material was available. In field

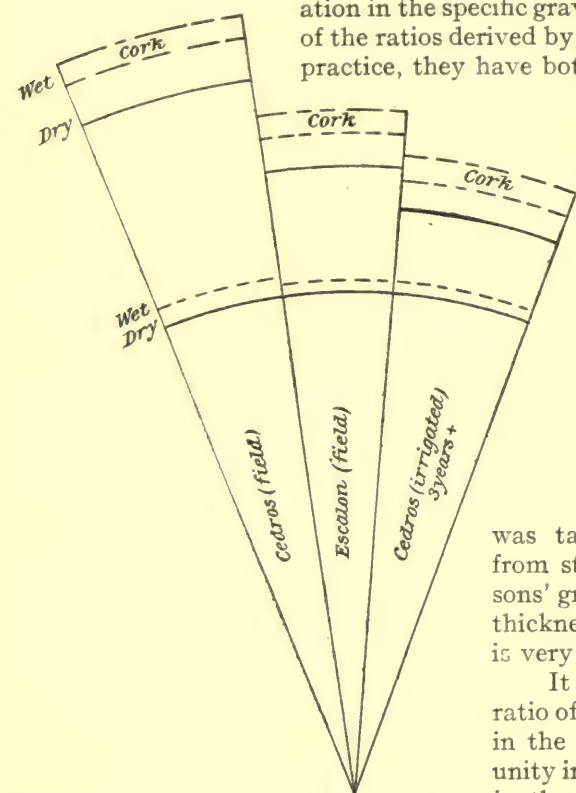


FIG. 17.—Relative thickness of cortex in stems of irrigated and field plants, the wood cylinders being of equal diameter when dry.

plants the ratio for the smaller twigs approaches 2.5, being reduced to 1.7 for stems 13 mm. in diameter, and still further, namely, to unity, for stems exceeding this diameter (20 mm. and more). From the economic point of view this material reduction of cortical tissues in irrigated plants is an important consideration, since it is these tissues which contain the rubber.

The ratios for the wet tissues indicate the large water-holding capacity of the irrigated cortex, especially as compared with the field material. These differences in volume are quite obvious in the radial measurements of the wood and bark. In tables 43 and 44 some accurately made measurements are given. The ratios are illustrated in figs. 15, 16. For the better direct comparison of field and irrigated plants dry twigs of the same initial total diameter were chosen and were measured both dry and after being soaked in water. The initial size is shown in the diagrams

by a half-circle. To the right of the vertical diameter is shown the irrigated plant; to the left of it the field plant. The upper quadrants show these when wet; the lower, when dry. To be noted are the greater capacity of the wood cylinder in field plants for swelling, due to the larger volume of the parenchyma rays; and the smaller capacity of the cortex tissues for swelling, due to the larger rubber-content. The greater volume of cork

TABLE 42.—*Volume of wood and cortex (Cedros, Sept. 1908).*

Irrigated plants.					Field plants.				
Diameter of wood cylinder.		Thick-ness of cortex.	Ratio of cortex to wood by volume.		Diameter of wood cylinder.		Thick-ness of cortex.	Ratio of cortex to wood by volume.	
Dry.	Wet.	Wet.	Dry.	Wet.	Dry.	Wet.	Wet.	Dry.	Wet.
mm.	mm.	mm.			mm.	mm.	mm.		
2.0	2.0	0.7	0.93	1.65	1.3	1.7	0.9	2.33	2.5
2.3	2.4	0.8	0.81	1.35	2.7	2.9	1.5	2.0	2.65
3.3	3.7	1.1	0.94	1.28	3.7	4.3	1.7	1.5	2.1
4.6	4.8	1.1	0.565	1.23	4.1	4.7	2.0	1.5	2.25
7.0	7.5	1.4	0.43	0.71	5.9	6.0	2.8	1.7	2.1
...	13.0	2.0	0.33	0.6	6.2	6.6	3.0	1.7	2.08
...	13.5	2.0	0.27	0.55	...	14.0	3.5	...	1.11
...	...	...	...	...	...	22.0	5.0	...	1.11
...	...	...	...	...	...	22.7	4.9	...	1.05

and of the cortical intercellular spaces in irrigated plants must also be considered. As these tissues are included in the tables under the term "bark," it is obvious that an error is introduced which is larger for the irrigated plants. Hence the ratios ought to be, for these, relatively smaller.

Table 44 shows the same relations for branches of larger size, in which the ratios of bark to wood are smaller, but relatively more so in irrigated plants. The figures are of special interest, as they include the ratio seen

TABLE 43.—*Transverse dimensions of terminal twigs of irrigated and field plants of the same initial size, before and after drying (fig. 15).*

	Total diameter.		Diameter of wood.		Thickness of cortex.		Thickness of cork.		Ratio of field to irrigated cortex, volume.	
	Dry.	Wet.	Dry.	Wet.	Dry.	Wet.	Dry.	Wet.	Dry.	Wet.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.		
(a) Irrigated..	2.6	3.45	1.85	2.0	0.375	0.725	0.13	0.16	1.71	0.95
(b) Field .....	2.6	3.15	1.5	1.7	0.55	0.725	0.10	0.10-0.15		
(c) Irrigated..	3.9	4.85	3.0	3.15	0.45	0.925	0.15	0.19	2.12	1.17
(d) Field .....	3.9	4.5	2.3	2.5	0.8	1.0	0.10	0.11-0.15		

in a plant from the Hacienda de San Isidro, near Escalon, Chihuahua, where guayule is said to grow rapidly. While the rate of growth is not as great as supposed, nevertheless it is sufficiently so to be reflected in the structure of the stem, which is intermediate in character between Cedros field and irrigated plants. In the three cases the initial wood cylinder diameter (20 mm.) was the same—in this way the largest available sizes could be compared. The thickness of the cork is, when wet, nearly the

same in all, though its irregularity makes accurate measurement impossible. When dry it is thickest in the Cedros field plant, thinnest in the Chihuahuan plant, and intermediate (though much more irregular in thickness) in the Cedros irrigated plant. The differences in the cortex are

TABLE 44.—*Comparative radial measurements, in millimeters, of medium-sized stems of guayule, wet and dry. Wood (dry) cylinder 20 mm. diam. in all. August 29, 1909 (fig. 16).*

Kind of plant.	Dry.			Wet.			Ratio of cortex to wood, by volume.
	Wood.	Bark (cortex + cork).	Cortex (without cork).	Wood.	Bark (cortex + cork).	Cortex (without cork).	
	mm.	mm.	mm.	mm.	mm.	mm.	
Cedros irrigated, 3 years old.....	10	1.7	1.3	10.25	2.5	2.0	0.28
San Isidro (near Escalon) field...	10	2.5	2.35	10.25	3.4	2.95	0.53
Cedros field.....	10	4.35	3.75	10.37	5.25	4.8	0.89

The irregularity in the thickness of the cork makes it difficult to measure it properly. It is, at all events, less than 1 mm., and relatively thinner in field plants.

apparent; the index of imbibition of the wood cylinder, while still greater in the Cedros field plants, is relatively much smaller than in smaller stems, because of the compression of the medullary rays.

Tables 45 and 46 are based upon comparative measurements of Cedros field and irrigated plants. The latter material, however, was collected in

TABLE 45.—*Relative amount of bark and wood in guayule, by volume (dry). Irrigated plants (Cedros, Apr. 1909).*

No.	Total diameter.	Diameter of wood.	Thickness of bark.	Ratio of volume of bark to wood.
	mm.	mm.	mm.	
1	15.0	13.0	1.0	0.32
2	9.12	7.32	0.9	0.48
3	8.3	6.7	0.8	0.50
4	5.8	4.25	0.77	0.79
5	5.6	4.35	0.62	0.70
6	5.22	3.75	0.735	1.00
7	3.5	2.6	0.45	1.00
8	2.4	1.4	0.5	1.46
9	2.15	1.4	0.37	1.11
10	1.52	0.95	0.29	1.67
11	21.7	18.6	1.55	0.31
12	12.4	10.9	0.75	0.40

Nos. 1 to 10, stems from single plant taken Apr. 1909. No. 11, stem from different plant taken Sept. 1908. This is the trunk (main) brought from Saltillo. No. 12, root from plant taken Sept. 1908. No. 8, base of piece through crowded nodes, bottom of 1909 growth, hence bark a little thicker here.

April 1909. At this time growth had only just recommenced, from which it is evident that the amount of water received between September 1908 (at which time I left Cedros) and the time of my later visit was very small—and the information obtained showed this to have been the case.

The chief value of these tables, besides indicating somewhat more fully the points already made, lies in the evidence they bear that the ratio



of bark to wood has increased during the period between the dates given above, as shown in brief in table 47.

As will be seen, this change in volume in the irrigated cortex is to be referred chiefly to an increase in the rubber-content.

TABLE 46.—*Relative amount of bark and wood in guayule, by volume (dry). Field plants (Sept. 1908).*

No.	Total diameter.	Diameter of wood.	Thick-ness of bark.	Ratio of vol. of bark to wood.	No.	Total diameter.	Diameter of wood.	Thick-ness of bark.	Ratio of vol. of bark to wood.
	mm.	mm.	mm.	"		mm.	mm.	mm.	
1	29.25	20.25	4.5	1.11	11	4.67	2.7	0.99	2.0
2	9.25	7.45	0.9	0.57	12	4.25	2.65	0.8	1.7
3	9.0	6.7	1.15	0.81	13	4.2	2.75	0.72	1.25
4	15.45	10.5	2.47	1.11	14	4.0	2.5	0.75	1.47
5	9.25	5.93	1.7	1.37	15	3.5	2.45	0.52	1.31
6	7.85	5.0	1.4	1.44	16	3.35	2.25	0.55	1.4
7	5.8	3.9	0.95	1.34	17	2.6	1.5	0.55	1.25
8	5.25	3.3	0.97	1.45	18	1.9	1.42	0.24	1.00
9	5.15	3.15	1.0	1.57	19	24.2	19.0	2.6	0.63
10	4.9	3.12	0.89	1.63	20	10.75	7.7	1.5	0.80

No. 1, basal portion of trunk; No. 2, a lateral root; No. 3, a tap-root; Nos. 4 to 18, series from a single plant; No. 19, San Isidro, Chihuahua, large plant; No. 20, Chihuahua, trunk, seedling.

A discrepancy which always appears between the ratios by weight, not here given, and by volume is greater for the irrigated plants on account of the larger rubber-content of the wood cylinder in the field plants.

The smaller ratios for the smaller twigs (Nos. 12 to 18 inclusive) for field plants in table 46 as compared with those in table 42 are due in part to the fact that the material was collected in the height of the growing-season, and hence the new growths have something of the character of the irrigated plant in its low rubber-content especially. The importance of this fact in its relation to practice is shown elsewhere.

TABLE 47.—*Ratios of bark to wood in Cedros irrigated plants collected in September 1908 and in April 1909.*

Date.	Range in size of stem (dry) diameter.	Limits of ratios for these sizes.
	mm.	
Sept. 1908 (table 42).....	3.4 to 9.8	0.93 to 0.43
Apr. 1909 (table 45).....	3.5 to 5.8	1.00 to 0.79
	3.5 to 8.3	1.00 to 0.5

It is interesting to note, further, that the ratios for root-tissues are similar in both types of plant, but are smaller in irrigated plants. They are also much smaller than those for the stem in each type. This fact should be considered in making up averages to indicate the relative economic value of cultivated guayule. The roots, in proper practice, should not enter into a calculation for returns in manufacture, and by excluding them the average ratios (those, namely, for stems only) are higher, but relatively higher for field plants, as shown in the tables above.

## EFFECT OF VARIOUS AMOUNTS OF WATER OF IRRIGATION.

The most fundamental economic question for which an answer will be sought in these pages is that relating to the production of rubber by plants under irrigation. As bearing upon the answer is the relation of the above tissue-responses to the amount of water supplied, as already indicated in table 44. That the inference based upon the data there displayed is correct is indicated by the measurements taken from irrigated plants from two localities where the conditions were unavoidably and markedly different, as follows:

*Cedros*.—Stocks planted March 1907, by Mr. C. T. Andrews. Irrigated freely till April 1908. Went dry till summer rains. 25 cm. growth during 1907 and during 1908. Long drought from September 1908 to May 1909, but probably irrigated somewhat during this period. Sample plant collected May 10, 1909 (plate 17, fig. B).

*Caopas*.—Whole plants of medium size planted January 1908, and abundantly irrigated till June 1908. On account of failure to start in January they were trimmed back down to the stouter branches. New shoots then started, these being for the chief part included above under "total diameter 3 mm. or less." The *Caopas presa* broke out in June 1908, so that between that date and the time of collection (May 9, 1909) no irrigation was possible (plate 46, fig B).

TABLE 48.—Comparison of ratios of bark to wood by weight for plants from *Cedros* and *Caopas*, irrigated.

Parts.	Cedros.	Caopas.
Stems, 3.0 mm. diameter.....	1.16	1.56
7 to 10 mm. diameter.....	0.89	1.20
Larger, up to 23 mm. diameter (wood cylinder) .....	0.525	0.84

From the figures it may fairly be concluded that the amount of disturbance in rate of growth in the tissues considered is, within certain wide limits, related to the amount of available soil-water. The less the water, the thicker the bark (cortex), and *vice versa*. The *Caopas* plants certainly had less water than the *Cedros* plants, and the ratios of bark to wood stand in these at 1.56 and 1.16, respectively, for the small branches which grew in both plants under irrigation. As to the reduction in radial measurement of the chief rubber-bearing tissue, the cortex, it must be remembered that this is compensated for by the more rapid growth of plants under irrigation (up to six times), so that the absolute amount of cortical tissue in an irrigated plant will be greater than that in a field plant for the same period of growth.

The rate of growth determines the total volume. In order to obtain an empirical factor for the purpose of conveying to the mind an approximate notion of the relative ability of field and irrigated plants to produce "bark" in a given period of time, I took two average twigs of one season's growth, removed the leaves, decorticated, and weighted. The figures in table 49 were obtained. Here it is evident that, aside from the much more rapid growth in weight in irrigated plants, the amount of rubber-

bearing tissue formed by a single twig is at least 5.5 times that produced on a field twig of similar age.

By introducing this factor, and that of rapid growth, into the calculation, it may be seen that the resulting total volume of the rubber-bearing

tissue preponderates in the most rapidly grown plants, and from the data set forth there emerges the conclusion that it is possible to regulate irrigation, and thereby to predetermine, within the usual limits approximately shown in the preceding pages, the relative total amount of cortex and wood. I do not forget that difficulties of another sort,

related to the manufacture of crude rubber, may be introduced, but with these we are not at present concerned. The remaining part of the question, as to the amount of rubber the tissues of irrigated plants are capable of producing, is in part answered beyond, in a succeeding chapter.

TABLE 49.

Source.	Weight of cortex.	Ratio of cortex of irrigated to field plant.
	grams.	
Irrigated plant..	5.44	} 5.6
Field plant .....	0.97	

#### EFFECT OF DROUGHT FOLLOWING IRRIGATION.

From the ecological point of view, it seems reasonable to argue that the greater production of parenchymatous tissues is in the direction of succulency, and is an adaptive response to the arid conditions under which the plant lives. The largest growth of these tissues is found in the parenchyma rays as well as in the cortex, and there can be little doubt that the parenchyma of the pith, parenchyma rays, and cortex function to some degree of efficiency as water-storage reservoirs. It is, however, clear from the measurements which have been presented in the foregoing tables that the way in which this succulency works is not by capacity for a large amount of water—irrigated plants are superior in this respect—but, it must be argued, in holding it more tenaciously. The efficiency in this direction is, however, not very great, if we measure it crudely, as when we observe the rate of wilting when the plant is removed from the ground, and it is not in any sense to be compared with the resistance of desert succulents in this regard. What the rubber itself may contribute to this moderate efficiency can be answered only in speculative fashion. The death of large numbers of plants scattered over large areas after severe drought does not warrant extravagant notions, at any rate.

#### EFFECT OF IRRIGATION ON THE PHYSICAL CHARACTERS OF THE WOOD.

The wood of irrigated plants is noticeably harder and more rigid than that of field plants (Lloyd, 1908*b*). This is apparent upon cutting or upon twisting or bending. For the purpose of measuring the differences in flexural rigidity, two slender wood cylinders of equal (2 mm.) diameter were obtained by freeing them from the cortical tissues, and were then subjected to bending before and after drying. It was found that, when still wet, the wood of the irrigated plant is three times more rigid than that of a field plant (the exact ratio was 11 to 3.5) and when dry the ratio is 2 to 1.



This mechanical difference appears to be due to the nature and extent of the medullary rays and their relation to the wood, together with the relative amount of mechanical tissue in the latter. The very great difference in the size of the parenchyma rays is seen in both transverse and tangential sections, as shown in the figures (plate 28, figs. 1, 2; plate 33, figs. 3 to 6), in which it is seen that the rays in field plants are very much larger than in irrigated plants. For this reason alone we must conclude, other things equal, that the former would be much the less rigid. Further, the walls of the medullary-ray cells in irrigated plants become much thickened and lignified (plate 33, fig. 7), while in field plants the cells remain thin-walled indefinitely, with the exception that there occur among them a very few tracheid-like cells (plate 33, fig. 8), with very peculiarly thickened walls. These are so few in number that it is difficult to attach any physiological or mechanical importance to them. The mechanical elements of the wood in the irrigated plants appear more compact to the eye, the lacunæ being smaller and the whole mass being made up of smaller and more regularly developed cells. It may here be remarked, also, that the development of medullary stereome is somewhat stronger, but this scarcely contributes a measurable quantity to the total rigidity of a stem more than 1 to 2 mm. in diameter.

The vessels of irrigated wood are frequently plugged with the so-called "Gummipropfen" at an age of two years or even less. Their appearance is hastened by artificial or by natural wounding, as the dying back of the peduncle. The pith-cells may undergo a considerable amount of sclerosis, without change of shape. The lumen is frequently very much reduced in size, and the walls are traversed by delicate branching canaliculi (plate 29, figs. 5, 6). Sclerosis of pith-cells occurs in *Manihot glaziovii* near the leaf-bases, that is, at the nodes (Calvert and Boodle, 1887), in the pith of *Liriodendron tulipifera* (Holm, 1909a), and in that of *Cornus florida* (Holm, 1909b). The sclerosed cells of the last-named are identical in structure with those of the guayule, both as regards the pores and the small size of the lumen. Jodin (1902) also notes a total sclerosis of the pith in *Cynoglossum officinale*, and partial in *Lithospermum fruticosum*. The sclerosis of pith-cells under irrigation suggests the value of experimentation with other plants in the reverse direction.

## THE PEDUNCLE.

It has been said elsewhere that the method of branching is correlated with the production of the inflorescences, the terminal new branches in twos or threes being produced by the outgrowth of the uppermost axillary buds below the peduncle. There is but little secondary thickening in the peduncle, while, correlated with its slender character, there is a large development of mechanical tissue (plate 34, fig. 1). In the young condition the chief points of difference between a peduncle and a definitive foliage stem are the absence of medullary canals<sup>1</sup> and the interruption of the hypodermis by the development of chlorenchyma, without, however, the reduction of the collenchymatic character. There are about 6 to 8 of these longitudinal chlorophyll strips, provided with numerous stomata with their axes placed longitudinally, as is usual. The cortex, which is, of course, primary, has usually 6 resin-canals above to 10 below. There are about a dozen bundles, and these, before secondary thickening is concluded, produce a few tracheids, though tracheæ are equally prominent constituents of the hadrome. A weak interfascicular cambium is formed, but its cells, without losing their cambial character, undergo sclerosis, preserving their rectangular transverse section. Stereome strands are formed, as in the stem, just within the pericycle and in the pith, but their relative amount of development is here much greater. It spreads toward the interfascicular cambium, involving the parenchyma-ray cells, sometimes entirely. The stereome within the cambium thus unites to form a complete stereomatic sheath, or perhaps is occasionally interrupted by incomplete sclerosis of parenchyma rays. Outside of the cambium, the sheath is interrupted by the cortical rays, inasmuch as the cells here do not become sclerotic, except a few adjacent to the leptome-stereome. The non-sclerosis of the interfascicular cortex comports with the view of the chiefly leptomatic origin of the stereome. The small amount of cortical stereome adjacent to the leptome-stereome may readily be recognized both by the color and shape of the cells.

In addition to the normal stereome, as this may be called, some of the pith-cells, a few of the outer cortical cells, and some also from the collenchyma become stereomatic. The chief part of this adjunctive stereome is derived from the pith, which contributes a notable amount to the inner surface of the mechanical sheath. In the basal part of the peduncle a periderm occurs, giving rise to a layer of cork about 0.1 mm. thick. No absciss tissue is formed, and the dead peduncle persists for years until disintegration finally overtakes it. As death extends toward the base of the peduncle, the vessels both of the peduncular wood and that of the adjacent stem become plugged, as elsewhere described. It is a matter of interest to note that the structure of the peduncle is very similar to that of the stem in the mariola (*Parthenium incanum*), and bears notable resemblances also to the herbaceous stems of *P. hysterothorus* and *P. lyratum*.

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<sup>1</sup> I have seen one canal in the pith on one occasion.

## THE LEAF.

## COTYLEDONS.

The cotyledons of the guayule are dorsiventral (plate 34, figs. 7 to 9). Both surfaces are free from trichomes. The parenchyma is composed of six layers of cells, of which the upper two form a palisade tissue. The spongy parenchyma is not highly differentiated, for the two lower layers of cells only have distinctive characters, and these are not pronounced.<sup>1</sup> There are no resin-canals in the blade, though the four primary canals of the hypocotyl pass, two into each of the petioles. The mid-vein (plate 31, fig. 1) in the petiole is composed of two mestome strands, the origin of which has already been discussed, but is single above, and there are two lateral veins. The cotyledons show certain well-marked responses to water and light conditions. The cotyledons of seedlings grown in the shade are slightly thinner than those of field seedlings, and have a much larger superficies (plate 34, figs. 6, 9). All the parenchyma cells, and all the epidermal cells save the guard-cells, are expanded in directions parallel to the surface. The epidermal cells of the surface are deeper also. The intercellular spaces of the spongy parenchyma are more extensive, and the cell-walls are thinner. These changes are in accord with observations in general, but it is of importance to note that the internal and external adjustments of the cotyledon are produced by changes in shape of the cells, and not by change in number of cells. This is well illustrated by the behavior of the epidermis, both as to the shape of the cells and the number of stomata. One might well suppose that there would be an increase in the number of stomata, as well as in their size, in plants well supplied with water and not subjected to severe aerial conditions. Counts of the stomata per unit of surface gave the results shown in table 50.

That is, the number of stomata per unit of area appears to depend on the amount of growth of the leaf. The greater number on the lower surface in the field plant is due to the rolled-leaf effect, which is absent from the shade plant. The result is that, in the plant which has to conserve water, there are relatively more stomata to carry it off.<sup>2</sup> Evidently therefore, the supposedly adaptive adjustments as regards the stomata do not involve their numbers in plants of the same species under different conditions. The thinner and less strongly cuticularized epidermis of the shade plant may indeed compensate, as may also the more extensive intercellular system, for the relatively fewer stomata. But inasmuch as the dampening of transpiration by stomata is not effective within wide limits (Lloyd, 1908a), such differences in numbers as the above may be of little or no significance.<sup>3</sup>

TABLE 50.

Surface.	Shade.	Field.
Upper . . . .	75	100
Lower . . . .	60	130

<sup>1</sup> The structure is very similar to that of the cotyledon of *Helianthus*, in which, however, the intercellular spaces are relatively more extensive, and there are more layers of cells.

<sup>2</sup> Transpiration rate is greater per unit of surface in sun plants than in shade plants (Bergen, 1908; Sampson & Allen, 1909).

<sup>3</sup> On this question the student should consult Renner, 1910.



That the structural adjustments of the cotyledon involve only change in shape of the cells is shown also by the responses of seedlings grown in a soil of high osmotic equivalent (plate 34, figs. 5, 8). Under this condition the surface of the cotyledon is greater than in the field plant (plate 34, figs. 4, 7), but its thickness is also much greater. The cells of the parenchyma are correspondingly deeper (plate 34, fig. 8), their extension of size being at right angles to the leaf-surface and parallel to the direction of greater extension of its size. This cotyledon represents the maximum response in a xerophytic direction, and it is worthy of note that under normal field conditions this response does not ensue, indicating that succulency here is primarily the effect of a soil condition, namely, the low physiological availability of the soil-water.

#### PROPHYLLS.

The earliest foliage leaves (prophylls) show a slight advance toward the bifacial condition, though normally they are dorsiventral. Nevertheless it is possible to induce a marked bifacial condition by growing seedlings in soil which contains a very meager supply of water (plate 35, figs. 5, 8). Such plants grow very slowly indeed, and the earliest foliage leaves attain but a small size and are relatively thick, while the resin-canals are of greater diameter. The extreme departure from this condition is shown by shade-grown leaves (plate 35, figs. 1, 2), with the greater superficial extent of which the shape and dimensions of their cells are correlated, while field seedlings and those grown in soil of high osmotic equivalent are very similar in structure. To be noted, however, both in these leaves and in the cotyledons, is the behavior of the spongy parenchyma. The lowermost layer of cells shows this especially. In shade plants (plate 35, fig. 1) the cells are broad, as viewed in a transverse section, and dumbbell-shaped. In the field plant (plate 35, figs. 3, 4) they are columnar and have two spaces between each two cells. In the seedlings exposed to distinctly unfavorable soil these spaces are almost, or frequently entirely, absent (plate 35, figs. 6, 7).

#### THE DEFINITIVE LEAF.

Although the foliage leaves exhibit a structural advance over the cotyledons, it is noticeable that, as compared with these, the definitive foliage leaves exhibit a smaller range of response. These have, to be sure, a dense clothing of trichomes, described elsewhere, and this fact may explain the difference, which receives no elucidation in the character of the stomata (plate 35, fig. 11). These show no special so-called adaptive features. There can be no doubt that closely packed hairs form an effective insulation which has the effect of producing mesophytic conditions, so to speak, over the leaf-surface, both by dampering transpiration and by modifying the sunlight.<sup>1</sup>

To determine the extremes of structural response within the leaf, I have taken one leaf from an irrigated plant during the period of rapid growth and one from a large seedling of good size after a six months'

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<sup>1</sup>Cf. Wiegand's interesting paper of 1910.

drought, as, presumably, final resultants of a complete antithesis of soil-water conditions. In these one observes a thinner leaf, though slightly more strongly cutinized, in the field plant (plate 35, fig. 13), otherwise but little difference is to be seen. In both the structure is strongly isolateral, with six layers of cells in each, but one may detect a somewhat more extensive system of intercellular spaces in the irrigated plant (plate 35, fig. 15), though it must be said that the difference appears but slight. The canals show no appreciable difference. Neither the stomata nor the substomatal spaces afford any ground for special comment, while the outer epidermal walls are, contrary to expectation, slightly thicker in irrigated plants. A denser trichome covering in the field plant may indeed compensate for this, but the observed differences are very slight.

It remains possible that differences in the character of the soil in which these plants grew are responsible for the close similarity, but the rate of growth in the irrigated plants and their resulting general mesophytic character minimize the value of the supposition.

## ABBREVIATIONS USED IN PLATES 22 TO 39.

<i>pc.</i>	pericambium.	<i>cot.</i>	cotyledon.
<i>end.</i>	endodermis.	<i>cor.</i>	cortex.
<i>ex.</i>	exodermis.	<i>r.c.</i>	resin-canal.
<i>l<sub>1</sub>, l<sub>2</sub>.</i>	primary and secondary leptome.	<i>ped.</i>	peduncle.
<i>h<sub>1</sub>, h<sub>2</sub>.</i>	primary and secondary hadrome.	<i>pr.</i>	parenchyma-ray (or cells of this).
<i>s.</i>	stereome.	<i>lib.</i>	libriform.
<i>m.c.t.</i>	median cotyledonary trace.	<i>l.</i>	lacuna.
<i>l.c.t.</i>	lateral cotyledonary trace.	<i>lp.</i>	leptome.
<i>c.t.</i>	cauline traces.	<i>pd.</i>	periderm.
<i>c.t.l.</i>	cauline traces, first primordial leaf.		

## DESCRIPTION OF PLATE 22.

- 1-5. Development of endodermal canals of root. Fig. 3, root 8 mm. diameter.
6. Lateral growth of endodermal cells and intercalated walls, with Caspary's band. Root 0.6 mm. in diameter.
7. Cortex (with exodermis) of a tap-root 0.46 mm. in diameter. First peridermal divisions in the hypodermal cells.
8. The reduction of cortical cells into cork has reached the endodermis.
9. Portion of a tap-root showing early cambium divisions.
10. The same in a somewhat older root to show development of intercalated mestome strand (*h<sub>2</sub>, l<sub>2</sub>*) at outer edge of primary hadrome plate (*h<sub>1</sub>*).
11. A still later stage showing closure of secondary hadrome about the parenchyma island by uniting with intercalated mestome strands. The separation of these from the primary plate is due to disturbance by the growth of a secondary root.
12. Primary leptome in contact with the endodermis, in the hypocotyl.
13. A secondary cortical canal arising in the phloem. The meatus is just at this moment appearing.
14. Details of secondary leptome, showing the relation of the resin-canal to the remaining elements. Root 4 mm. in diameter.
15. Pores in walls of endodermal and cortical cells (*cf.* plate 41, fig. 2).
16. Pericambium in a root after primary stereome has begun to develop.





## DESCRIPTION OF PLATE 23.

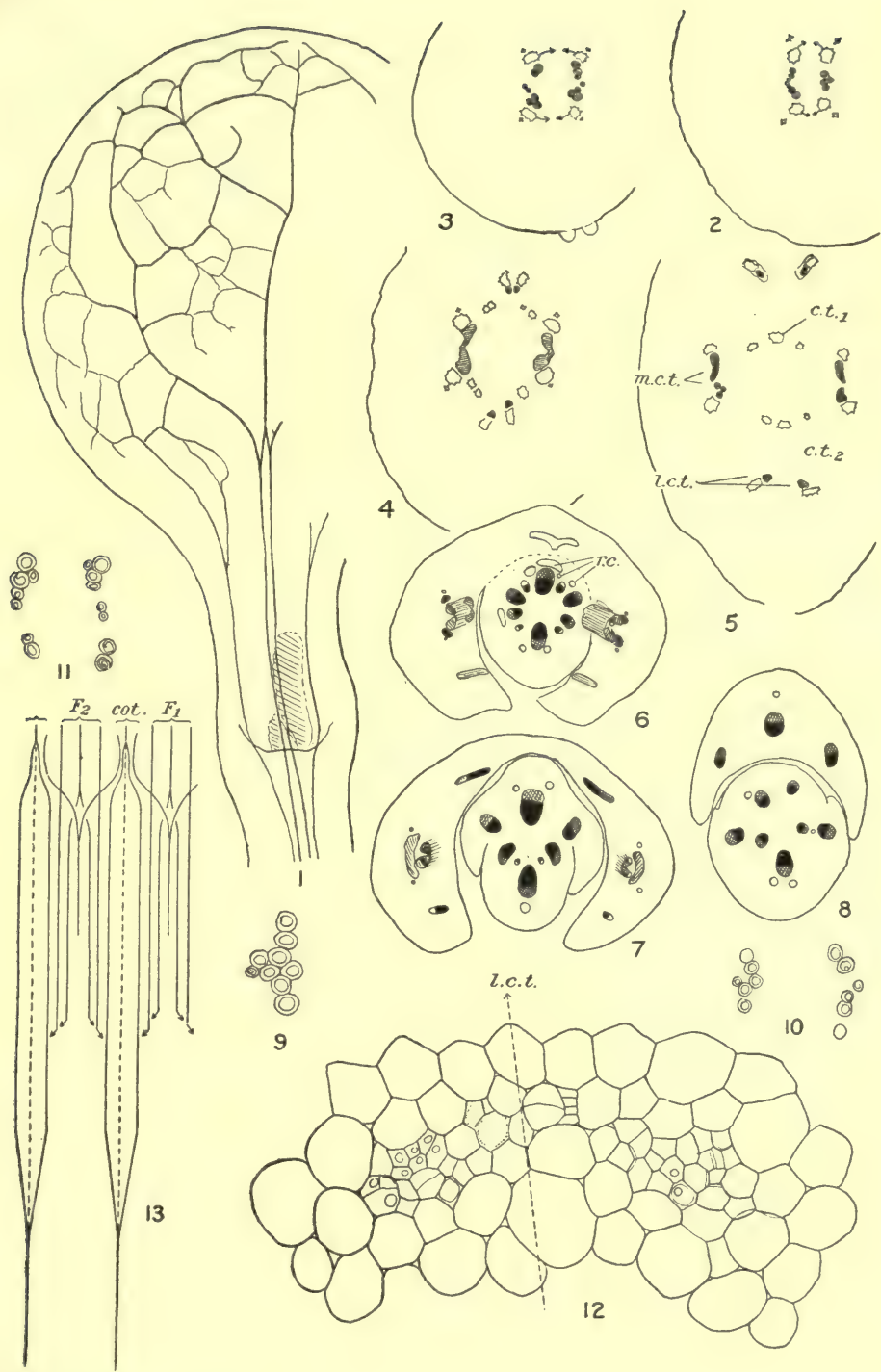
- 1-7. Tap-root.
  1. Field seedling.
  2. Irrigated seedling.
- 3-5. Field seedling, 2 mm. diameter (*cf.* plate 40, figs. 2, 3).
  3. Sector to show arrangement of tissues and distribution of rubber.
  4. Endodermis and pericambium of a root 1.2 mm. in diameter.
  5. Same, thickened and compressed; root 1.5 mm. in diameter; globules of rubber.
6. Region just within primary canals. Primary leptome-stereome ( $s_1$ ); secondary leptome-stereome ( $s_2$ ).
7. Parenchyma ray enlarged to show globules of rubber.
8. Epidermis of the hypocotyl, first peridermal divisions.
9. Trichome from hypocotyl.





## DESCRIPTION OF PLATE 24.

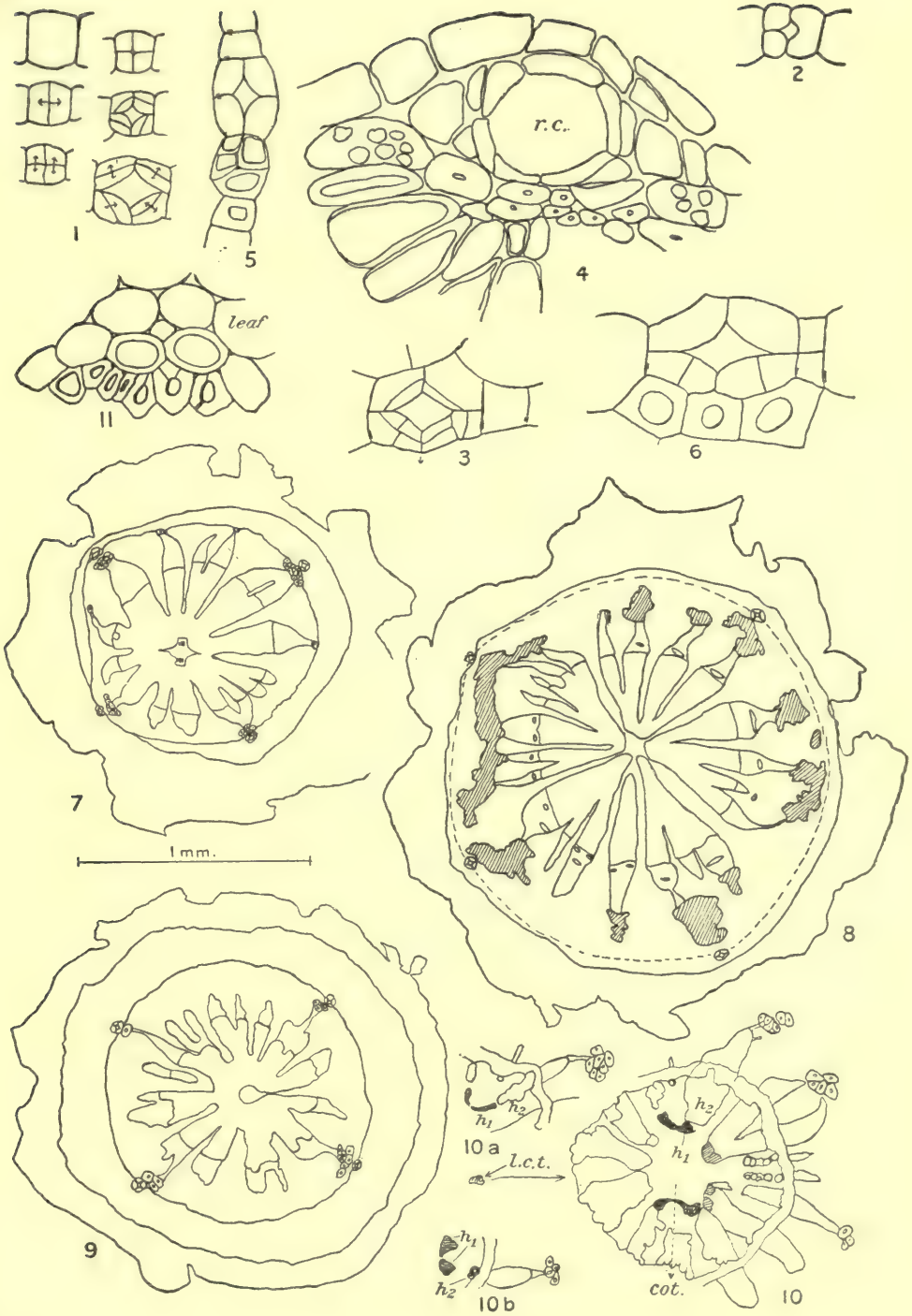
1. Cotyledon *en face*, to show distribution of vascular strands.
- 2-5. Sections through cotyledonary collar and upper part of hypocotyl in an ascending series.
6. Section through cotyledonary collar, and lower part of first internode.
7. Section through first node of epicotyl.
8. Section through stem near second node of epicotyl.
- 9-11. Section through different levels to show primitive trachea and its relations to older elements.
9. Base of hypocotyl.
10. Middle of hypocotyl.
11. Base of cotyledonary collar.
12. Origin of cauline strands at a level between those of figs. 4 and 5, but in a younger specimen.
13. Diagram of the vascular tissue (hadrome) in the plantlet. Arrows indicate fusion; dotted line the primary trachea.



## DESCRIPTION OF PLATE 25.

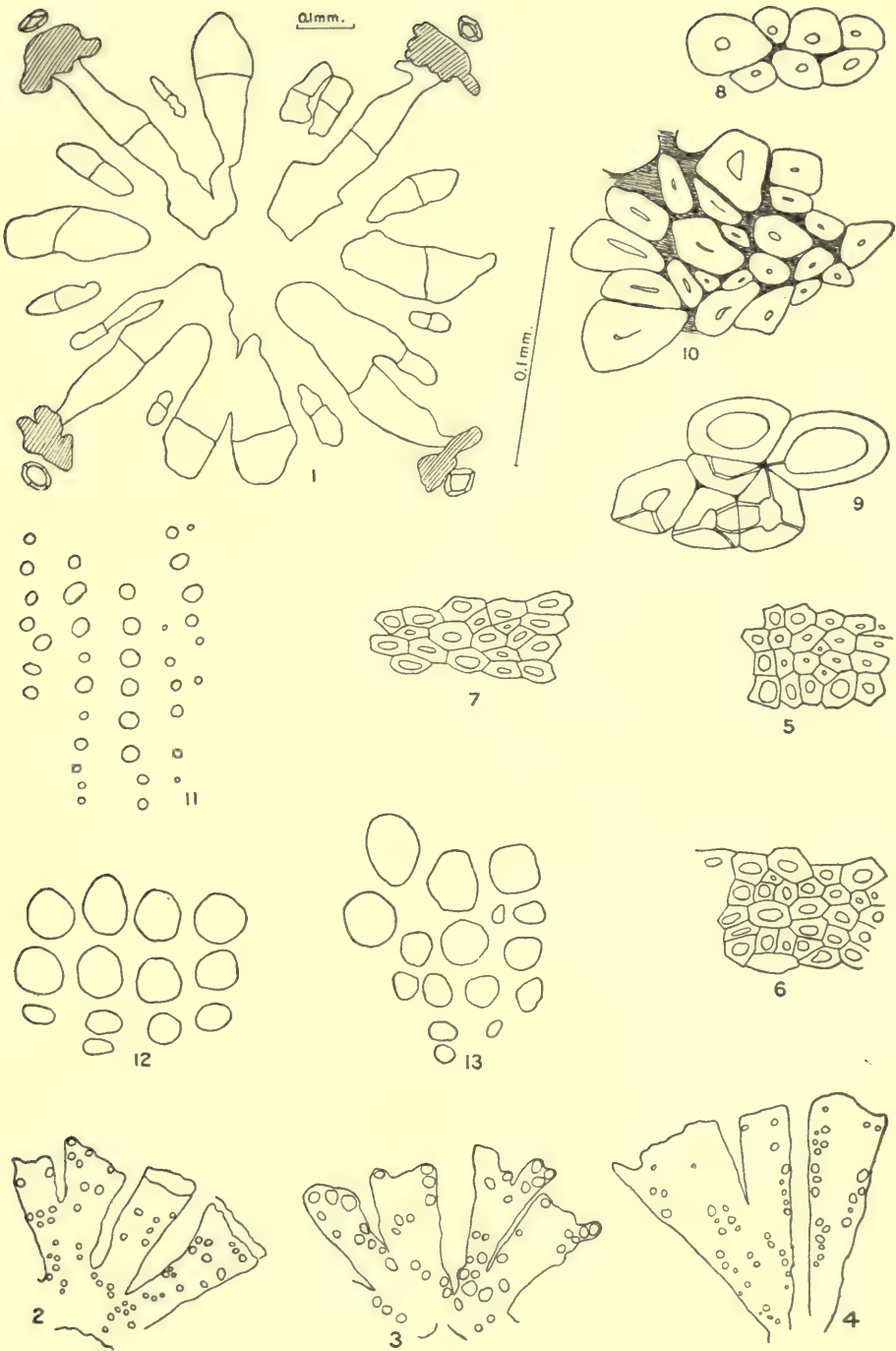
- 1-6. Primary endodermal resin-canals of the hypocotyl.
  1. Cell lineage (diagrammatic).
  2. A not infrequent but abnormal behavior.
  3. Definitive condition, as regards cell-walls.
  4. Definitive condition after growth and readjustment.
  5. Endodermic stereids adjacent to canals.
  6. Stereids (pericyclic?) just within canal in stele.
- 7-10. Transverse sections; hypocotyl.
  7. Field seedling, 1.8 mm. diameter.
  8. Irrigated seedling of slow growth. Secondary splitting apart of wood cylinder.
  9. Etiolated seedling 2 mm. diameter.
  10. Etiolated seedling 2 mm. diameter. Hypocotyl through cotyledonary collar. Secondary hadrome of cotyledonary median traces is morphologically cauline and distinct from primary tissue. *l. c. t.*, Lateral cotyledonary trace passing out from the stele.
- 10a, 10b. Cotyledonary, median traces at another level.





## DESCRIPTION OF PLATE 26.

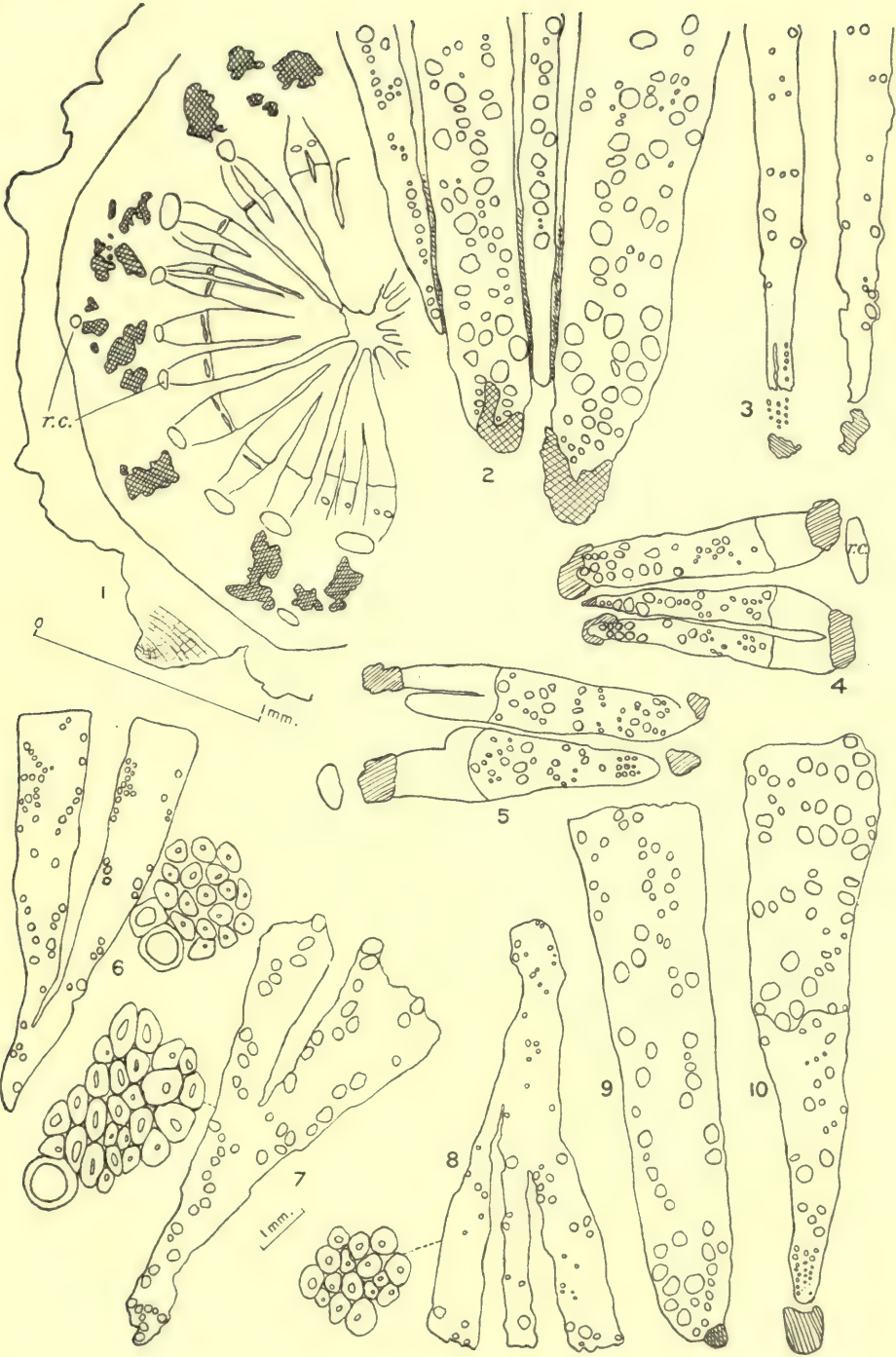
1. Hypocotyl of an etiolated seedling: the stele, showing rupture of wood column and secondary opening of medullary rays.
- 2-4. Sectors of the hadrome to show relative amount of conductive and mechanical tissue.
  2. Field seedling.
  3. Etiolated seedling.
  4. Irrigated seedling of slow growth.
- 5-7. The mechanical tissue (libriform) of hadrome of above.
  5. Field seedling.
  6. Etiolated seedling.
  7. Irrigated seedling.
- 8-10. Stereome (leptome) of above.
  8. Field seedling.
  9. Etiolated seedling.
  10. Irrigated seedling.
11. Protohadrome of a field seedling; the size of the lacunæ.
12. Same; base of a peduncle, irrigated
13. Same; an irrigated plant, 2 cm. from apex.





## DESCRIPTION OF PLATE 27.

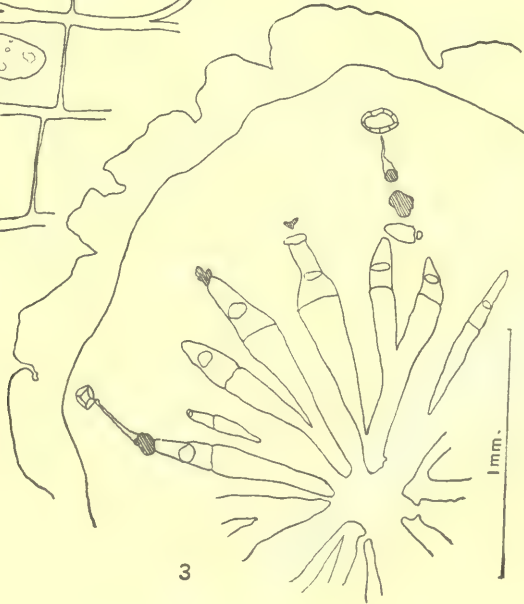
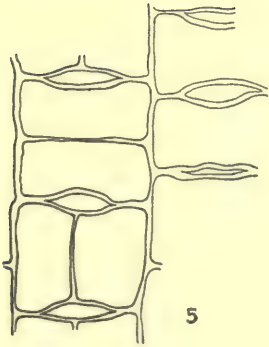
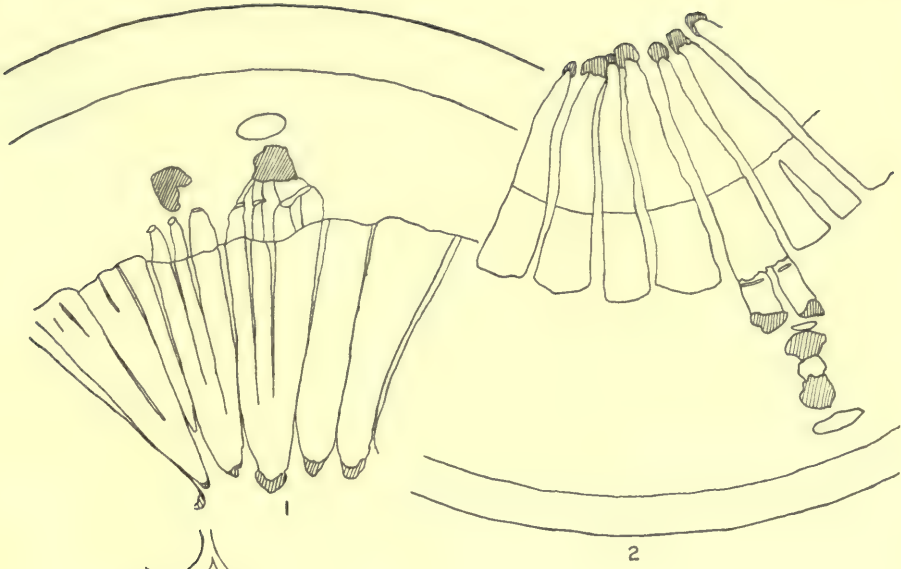
1. Hypocotyl, irrigated seedling of very rapid growth, about 2 months old.
2. Wood of irrigated stem 6.5 mm. in diameter.
3. Wood of field stem 8 mm. in diameter. (Figs. 2 and 3 are drawn to same scale.)
4. An irrigated stem.
5. Growth of 1907, terminal twig of a very large field plant. (Figs. 4 and 5 are drawn to same scale.)
6. Irrigated seedling of very slow growth.
7. Irrigated seedling of very rapid growth.
8. Field seedling. (Figs. 6 to 8 are drawn to same scale; the total wood to the scale shown, libriform to a larger scale.)
9. Base of growth of 1908, Cedros, irrigated plant, 1 year's growth.
10. 2 years' growth (1906-07), field plant, Cedros. (Figs. 9 to 10 are drawn to same scale.)



## DESCRIPTION OF PLATE 28.

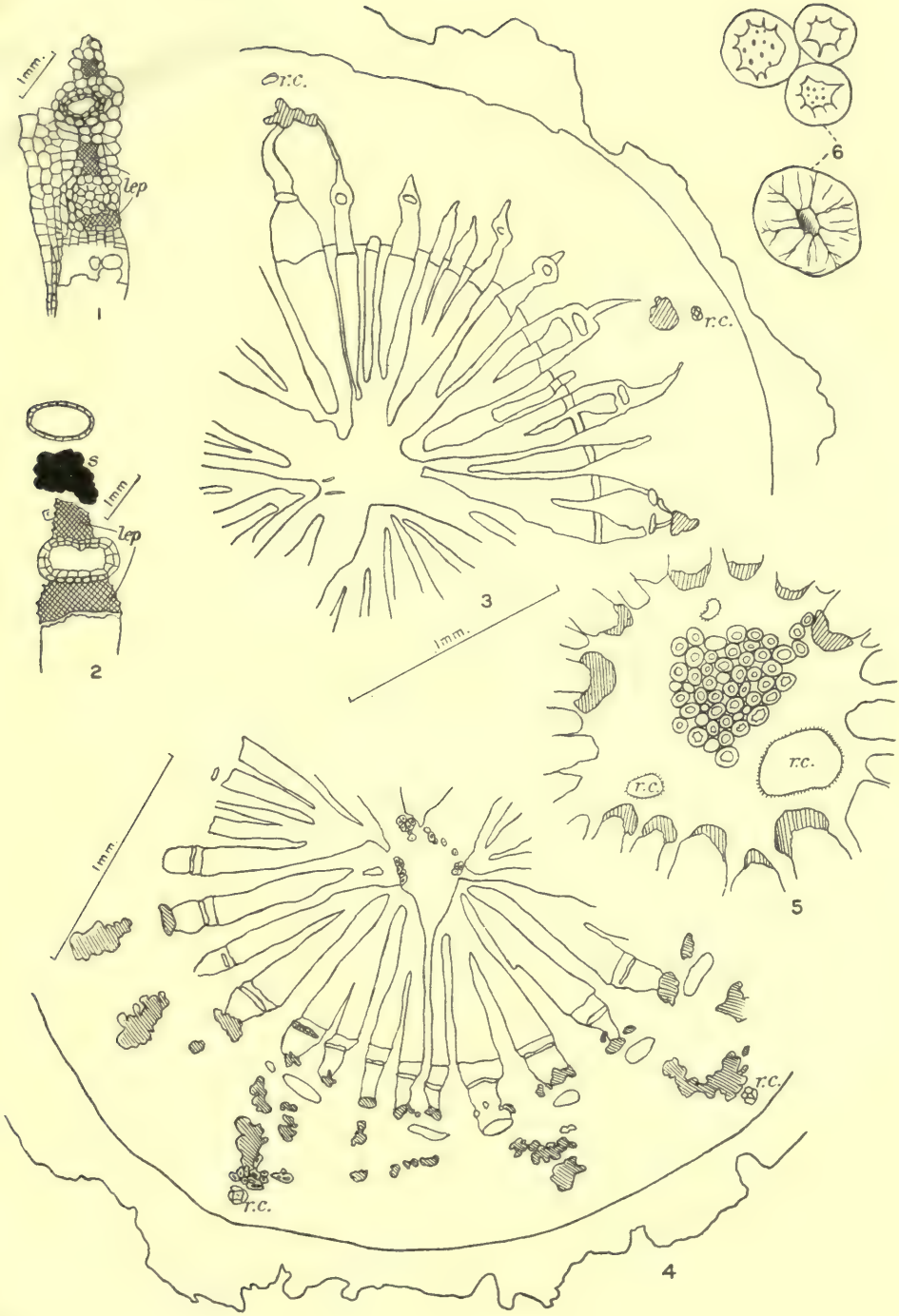
1. Irrigated plant, stem 1 year's growth.
2. Field plant, stem 2 years' growth. Note width of parenchyma rays and depth of cortex. (Figs. 1 and 2 are drawn to same scale.)
3. Hypocotyl, field seedling less than 1 year old.
4. Cortex of hypocotyl after secondary enlargement. Transverse section.
5. Cortex of root; tangential section.





## DESCRIPTION OF PLATE 29.

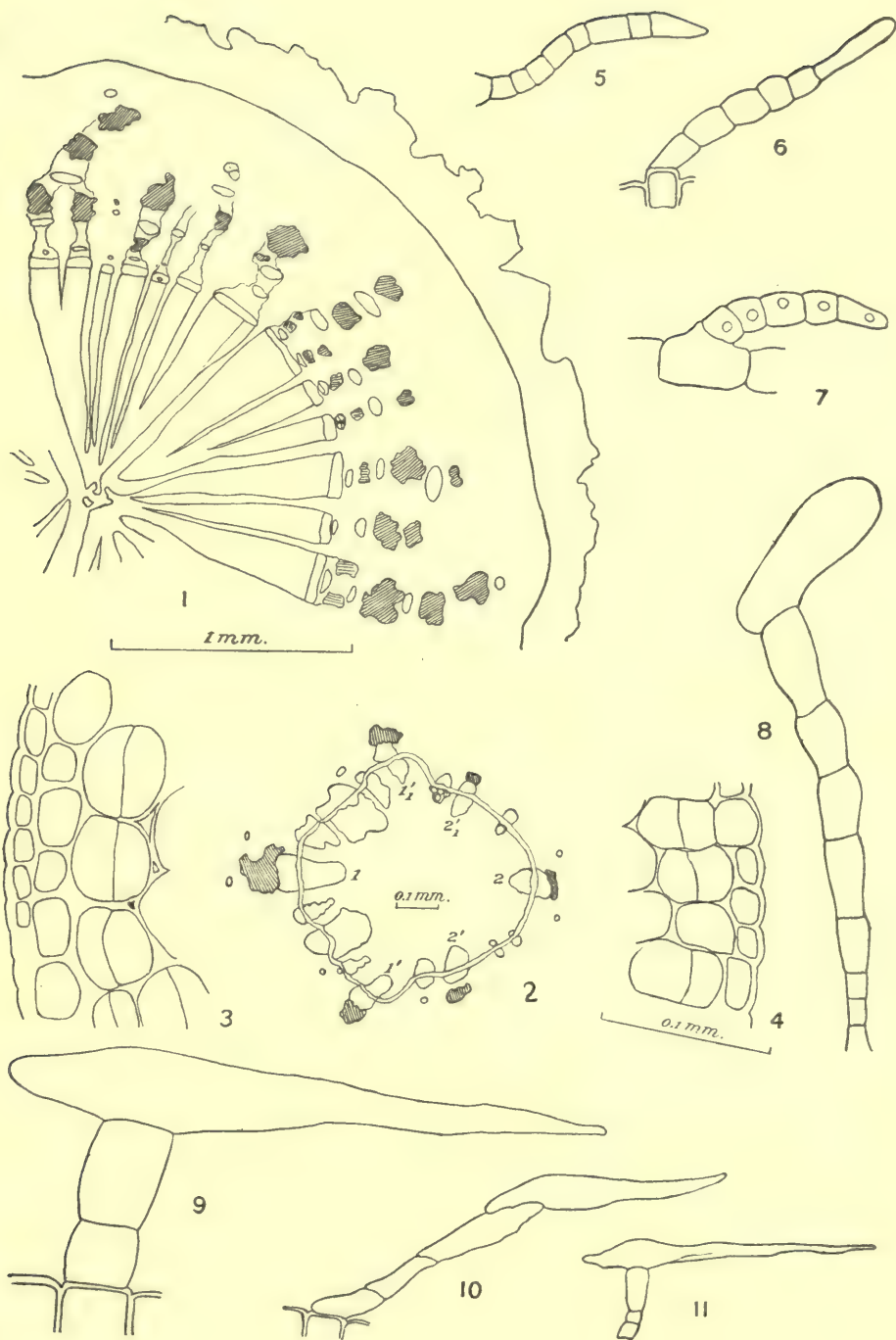
1. Leptome region of hypocotyl shown in fig. 3.
2. Leptome region of hypocotyl shown in fig. 4.
3. Hypocotyl, irrigated seedling of very rapid growth.
4. Hypocotyl, irrigated seedling of very slow growth.
5. Pith, Cedros irrigated stem, showing sclerosed pith-cells.
6. A few of these cells in detail.





## DESCRIPTION OF PLATE 30.

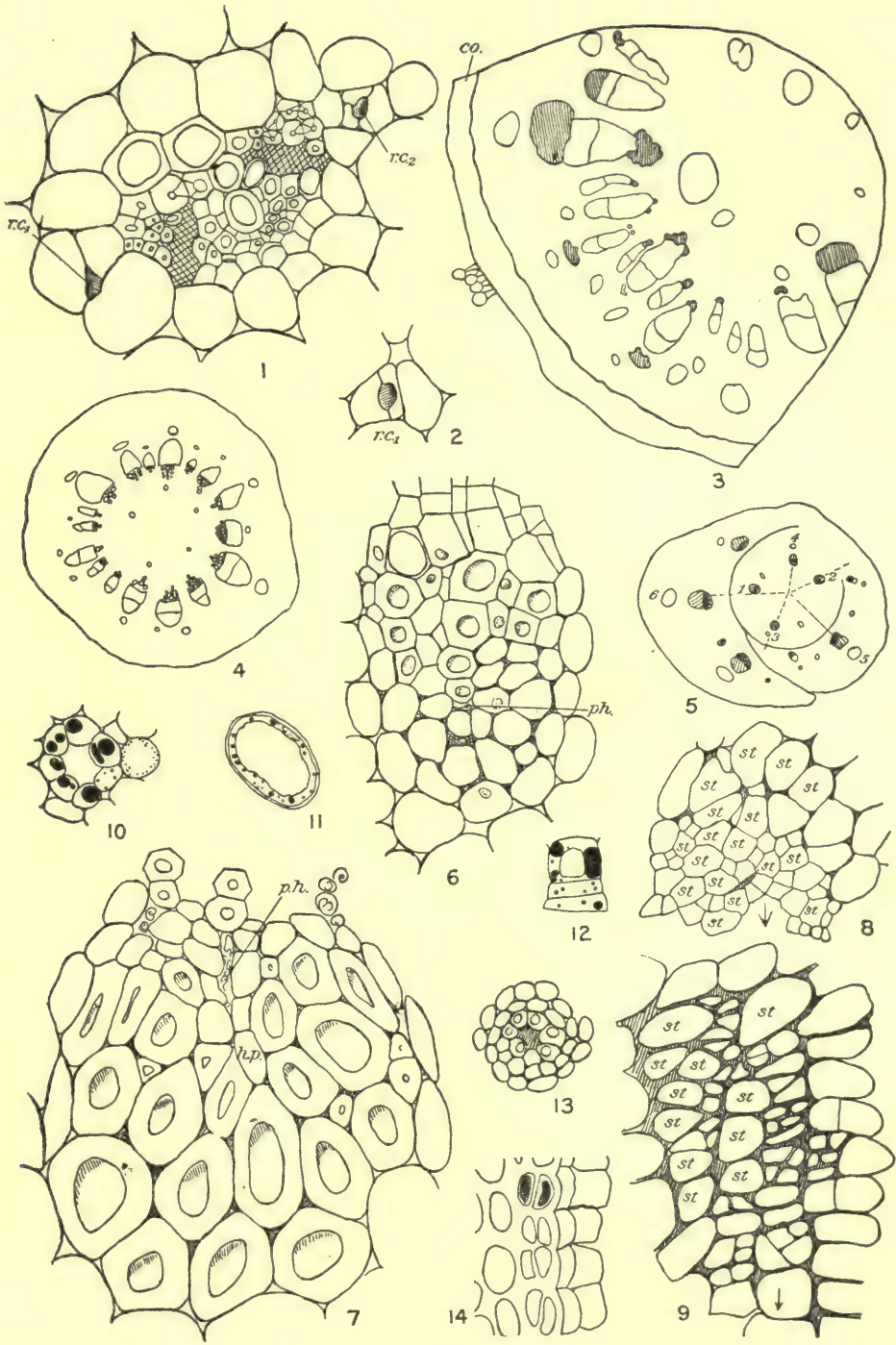
1. Hypocotyl, field seedling for station 2, April 1909, less than 8 months old.
2. First internode, epicotyl; the primary stereome bundles.
3. Periderm opposite bundle 1 in fig. 2.
4. Periderm opposite bundle 2 in fig. 2.
- 5-11. Trichomes.



## DESCRIPTION OF PLATE 31.

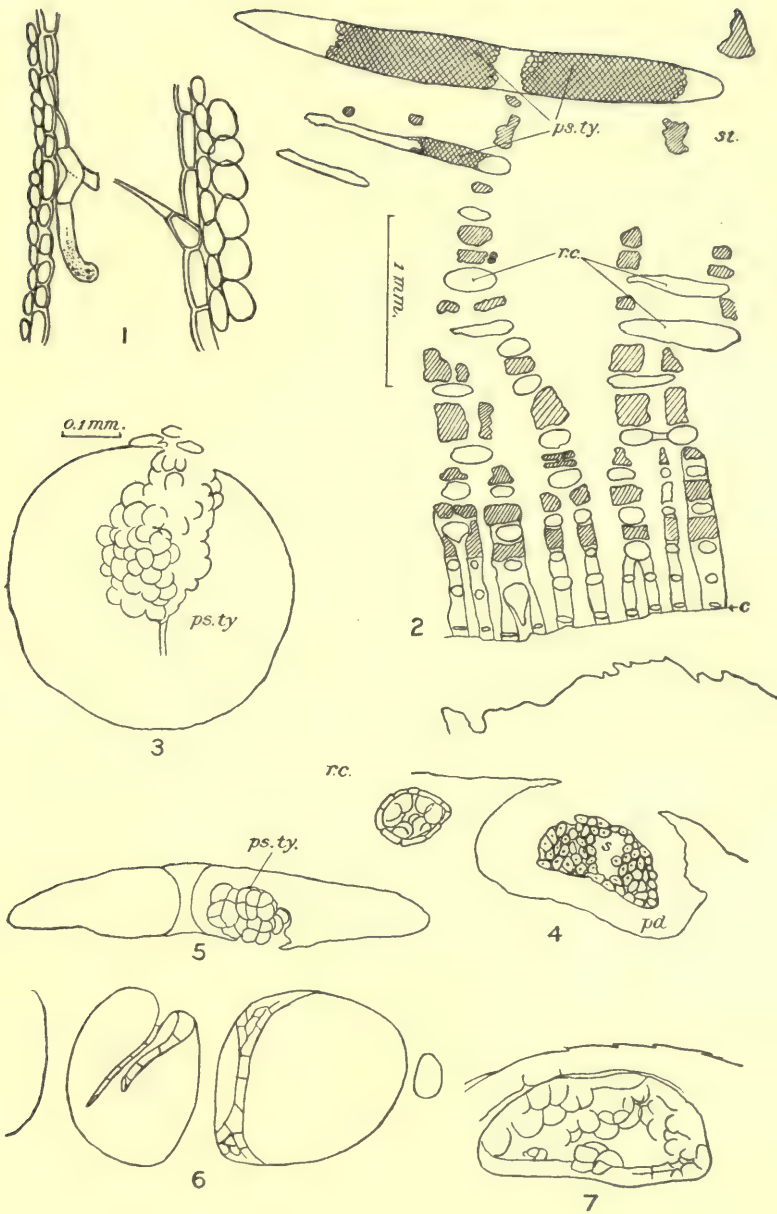
1. Transverse section through upper part of petiole of a well-matured cotyledon, in which one sees the ends of the resin-canals,  $rc_1$ ,  $rc_2$ . Above this level they end blindly.
2. A section of one of the resin-canals ( $rc_1$ ) in fig. 1, somewhat nearer base of same cotyledon.
3. Transverse section 3 mm. from apex of stem of a field plant. *co*, cork. Slow growth.
4. Transverse section through a stem in rapid growth 2 mm. below apex. The five medullary canals are established according to a  $2/5$  phyllotaxy.
5. A section through a stem apex above that of fig. 4, in which the order of development of the cortical canals is seen to relate to that of the leaves.
6. Inner part of hadrome bundle of stem, showing cells which become stereids.
7. The same, in which the stereids are of maximum size and their walls partially thickened. (Figs. 6 and 7 are drawn to the same scale.)
8. Enlargement of stereid elements in leptome previous to thickening of walls.
9. The leptome in which the primordial cells which become stereids, *st*, are seen.
10. A very young medullary resin-canal in the secretory cells of which are seen relatively large globules of rubber. Minute ones appear in adjacent cortical cells.
11. One of these cortical cells on a larger scale, to show the rubber granules more exactly.
12. Secretory cell of medullary resin-canal after periclinal divisions, showing granules of rubber.
13. The schizogenous origin of the medullary canal.
14. Peridermal divisions in the collenchyma.





## DESCRIPTION OF PLATE 32.

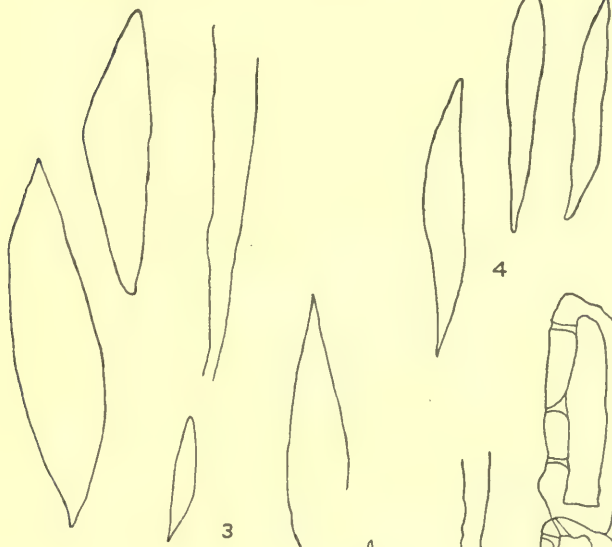
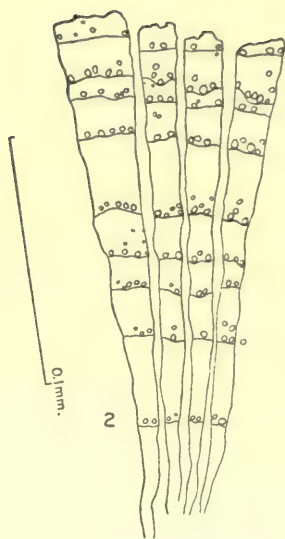
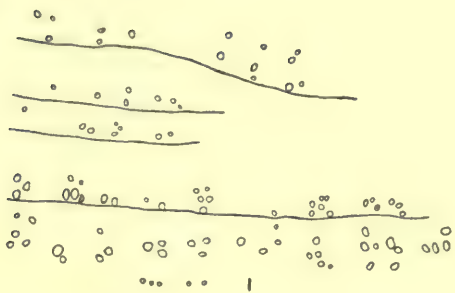
- 1, 6. Sections of resin-canals in which trichome-like structures occurred.
2. Transverse section through a 20-year-old cortex.
3. Pith-canal with pseudotylose.
4. Primary cortical canal of the stem with pseudotylose; the spread of periderm (*pd.*) about a stereome bundle is shown.
5. Pseudotylose in an old cortical canal.
6. Trichome-like columns formed in pith in seedlings of slow growth.
7. Primary (endodermal) root canal with pseudotylose.





## DESCRIPTION OF PLATE 33.

1. Annual rings in duramen of an old stem.
2. Annual rings in the wood of an 8-year-old stem.
- 3-4. Parenchyma rays as seen in a tangential section of a stem of a field plant.
- 5-6. Same, irrigated plant.
7. Sclerosed parenchyma-ray cells of an irrigated plant.
8. Tracheidal parenchyma-ray cell of a field plant.
9. Libriform of an irrigated plant; old wood.
10. Same, field plant; old wood.



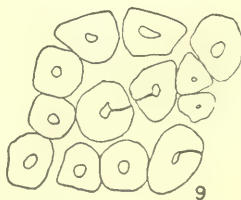
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8



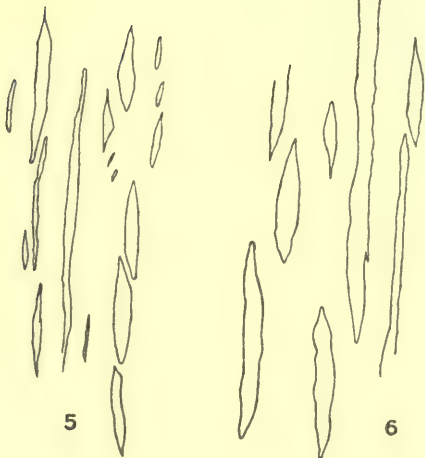
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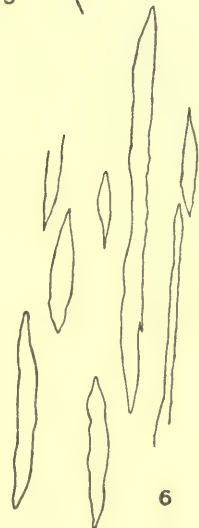
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10



5

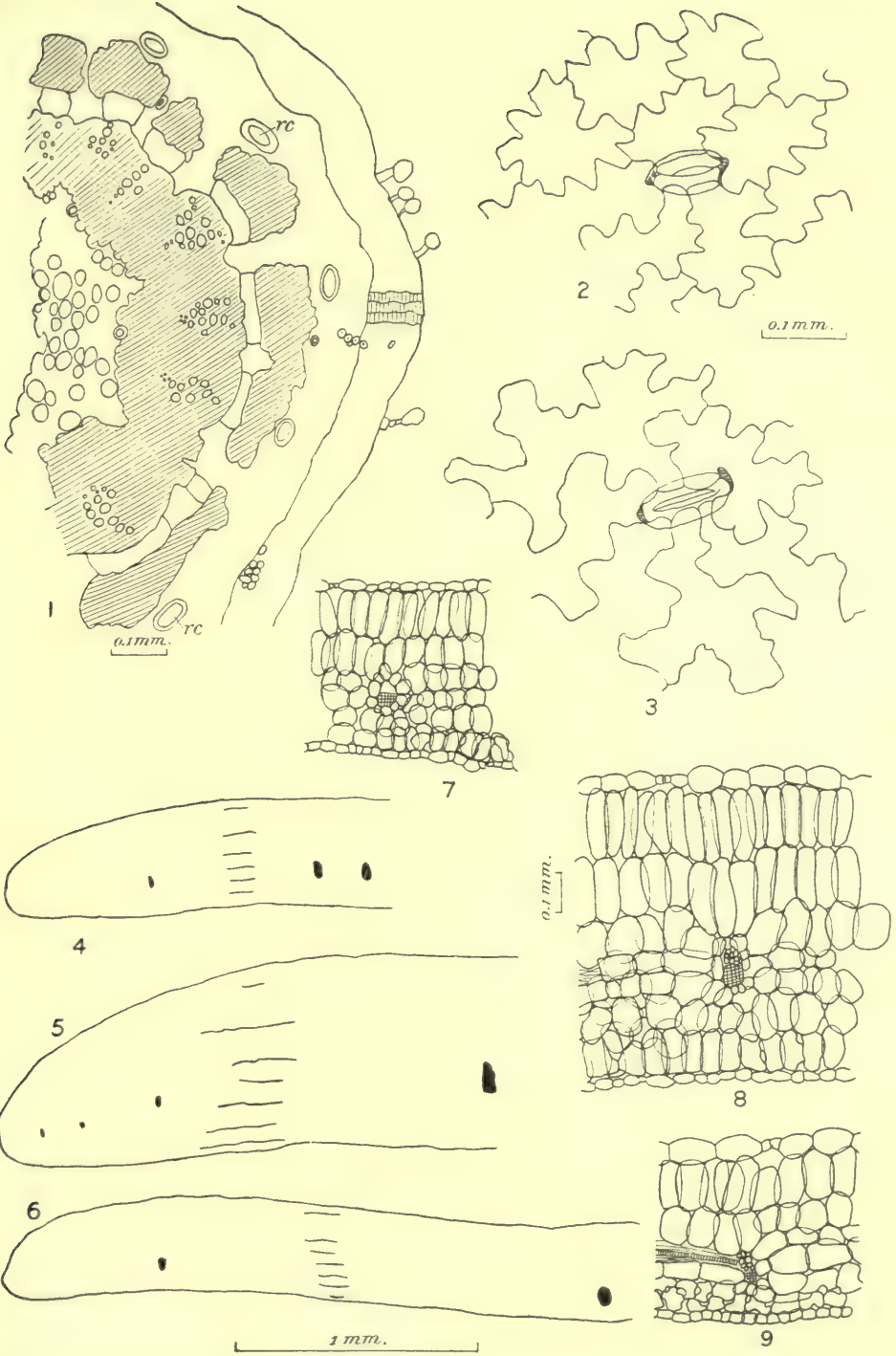


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## DESCRIPTION OF PLATE 34.

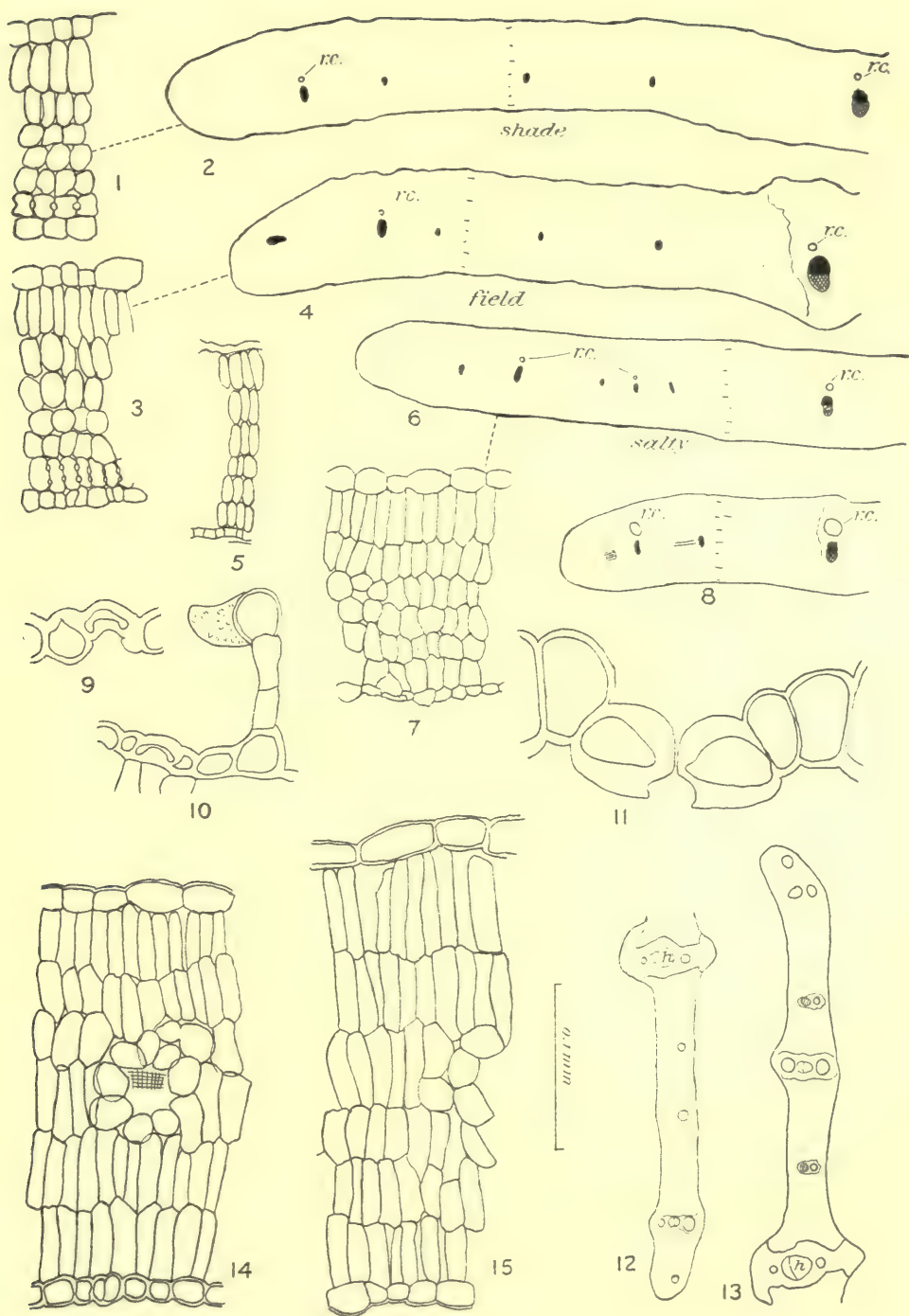
1. Transverse section of a peduncle. The mechanical tissues are hatched.
2. Lower epidermis of the cotyledon of a field seedling. To accompany figs. 4 and 7.
3. Same, seedling grown in shade (to accompany figs. 6 and 9).
- 4, 7. Cotyledon of a field seedling.
- 5, 8. Cotyledon of a seedling grown in soil with a high saline content.
- 6, 9. Same, grown with abundant water and shade.





## DESCRIPTION OF PLATE 35.

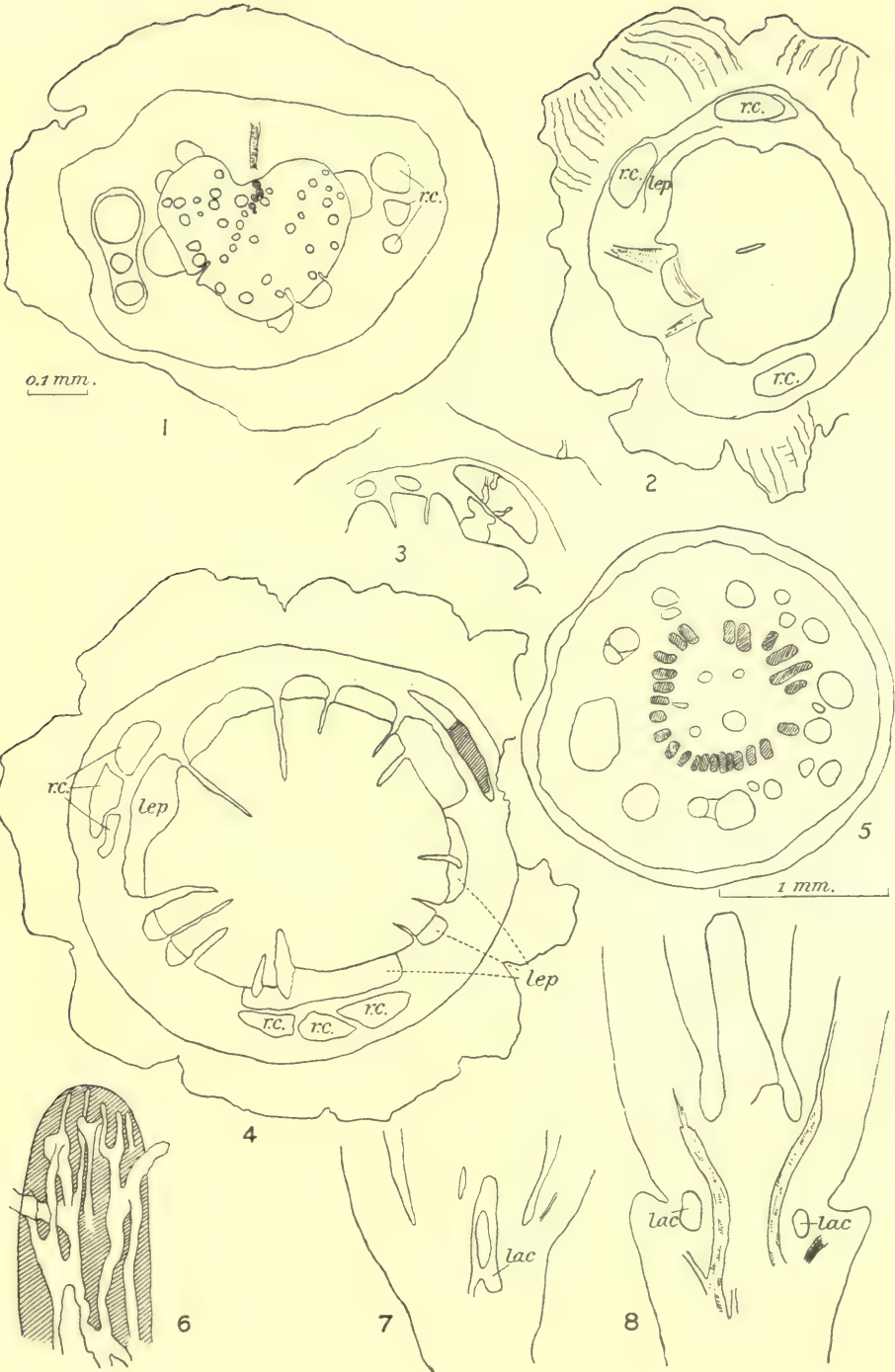
- 1-2. First primordial leaf, seedling grown in shade.
- 3-4. Same, field.
- 5-8. Same, seedling under irrigation (exp. 141, May 1908).
- 6-7. Same, in strongly saline soil.
  - 9. Epidermis of a field plant (Station 2).
- 10. Same, irrigated plant.
- 11. Stoma of leaf, figs. 6-7.
- 12. Transverse section, definitive leaf; field (Station 2, April 1909)
- 13. Same, irrigated. August 1908.
- 14. Detail of fig. 12.
- 15. Detail of fig. 13.





## DESCRIPTION OF PLATE 36.

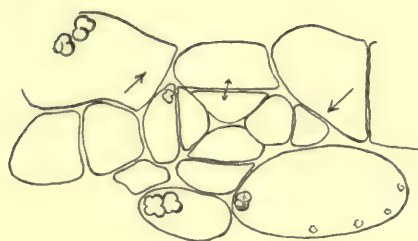
1. Transverse section, lower end of a tap-root after considerable secondary thickening, to show large size of primary canals.
2. Same, diarch secondary root.
3. Detail, to show thin secondary cortex and secondary canals.
4. Triarch secondary root.
5. Stem of slow growth. The large size of the cortical canals is notable.
6. Diagram of the medullary canals at the apex of a slowly growing stem.
7. Early anastomosis of primary cortical canals, parallel to the plane of the cotyledons.
8. Same, at right angles to the plane of the cotyledons.



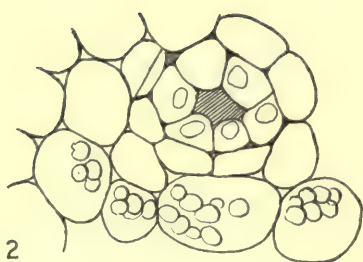
## DESCRIPTION OF PLATE 37.

- 1-5. Primary cortical canals.
  1. Endodermal origin in a young epicotyl. This canal has been rotated, but not displaced otherwise.
  2. Etiolated seedling-epicotyl. Lateral displacement, but not sufficient to mask its relation to the endoderm.
  3. Displacement sufficient to mask origin.
- 4-5. First internode. An earlier and later stage in the derivation of the cortical canal from the endodermis. The endodermal origin is masked by indefinite character of endodermis.
- 6-7. Later and earlier conditions of ventral foliar canal. *xy* indicates the position of the hadrome of the mid-vein.
8. Cortical canal in *Parthenium incanum*. The endodermal origin is clear.

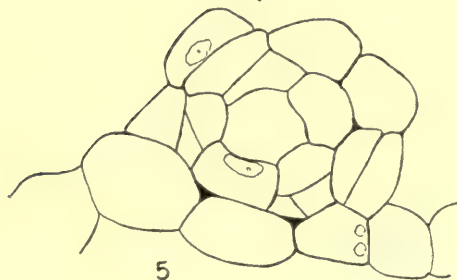




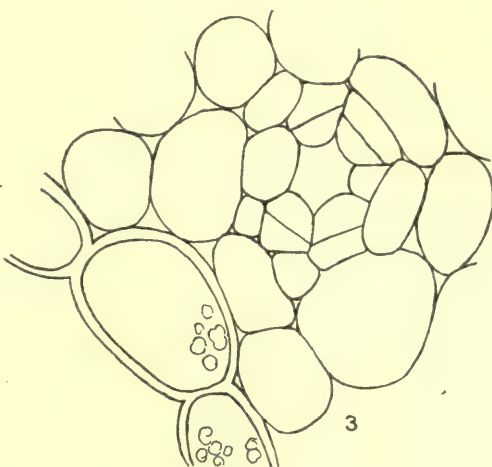
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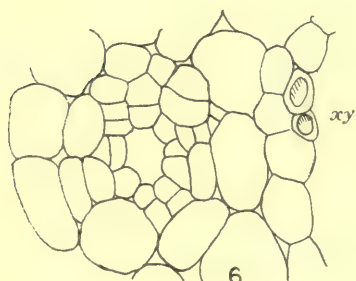
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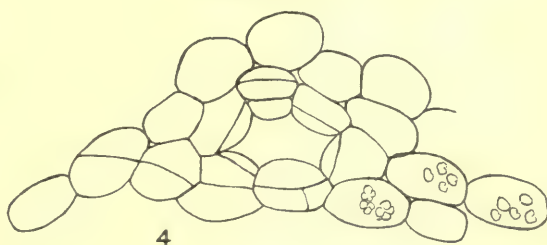
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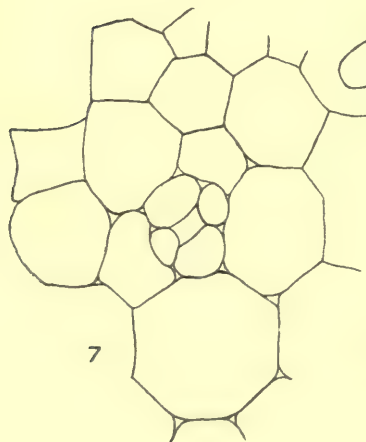
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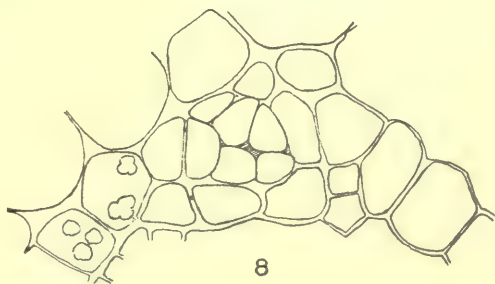
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4



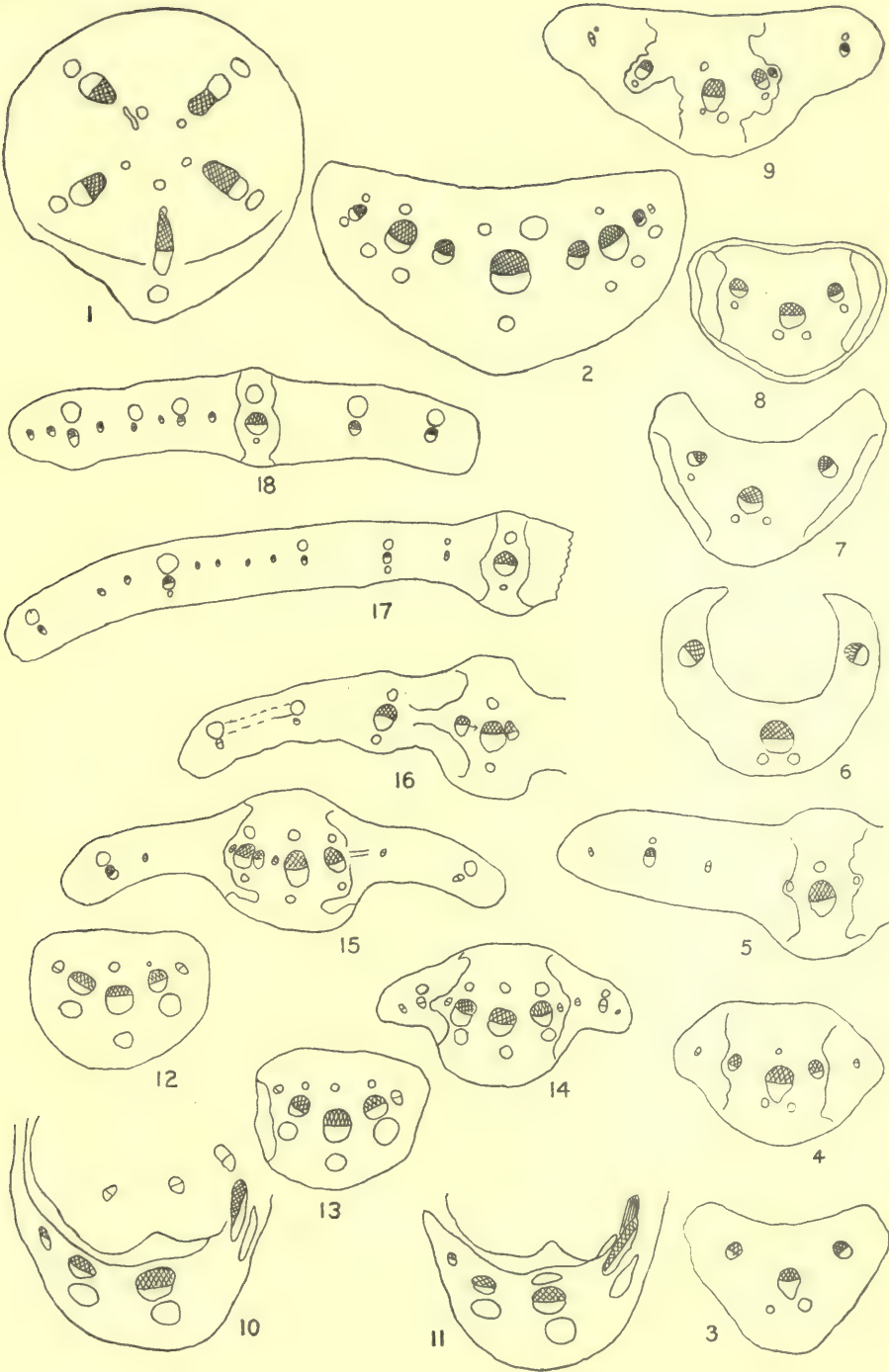
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## DESCRIPTION OF PLATE 38.

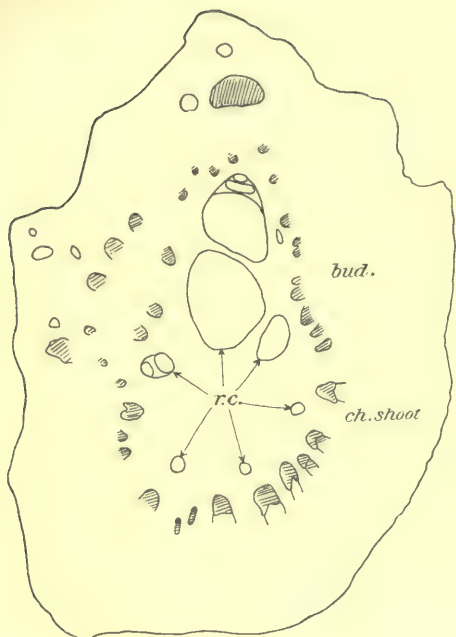
1. Transverse section, definitive stem, to show primary plan of canals.
2. Petiole, to show the canals of a large foliage leaf. Dorsal canals of cauline origin. Ventral canals, foliar.
- 3-5. First foliage leaf.
- 6-9. Another (first) foliage leaf.
- 10-18. Definitive leaf.



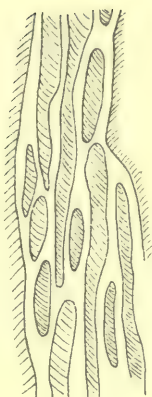


## DESCRIPTION OF PLATE 39.

1. Chief (foliage) shoot and axillary bud. Medullary canals in both.
- 2-3. Successive planes through chief peduncular shoot, and axillary bud, field plant. All canals pass into bud.
- 4-7. Successive planes from below upwards of an irrigated chief (peduncular) shoot and axillary bud. Two medullary canals which have passed into the bud branch to form four canals.
8. Secondary cortical resin-canals in old cortex. Tangential section.



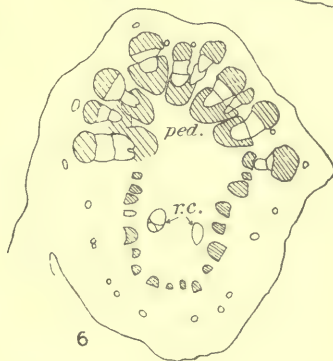
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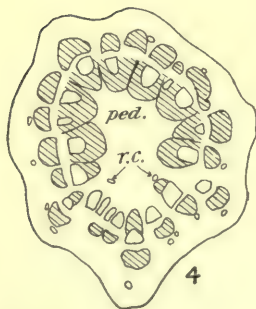
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## CHAPTER VI.

### THE RESIN-CANALS IN THE GUAYULE.<sup>1</sup>

#### THE CANAL-SYSTEMS.

Because of the comparative interest of the facts involved it is here proposed to summarize my observations on the origin, structure, and distribution of the resin-canals in *Parthenium argentatum*. The canals occur in this plant in well-defined systems,<sup>2</sup> as follows:

(a) Primary systems:

1. In the cotyledons, the hypocotyl, and the root, a continuous system.
2. Independent of this, the systems in roots of secondary and higher order.
3. In the cortex of the stem and in the dorsal moiety of the leaves, forming a continuous system.
4. An independent<sup>4</sup> system in the dorsal moiety of the leaf.
5. An independent<sup>4</sup> system in the ventral moiety of the leaf.
6. In the pith of the stem: the medullary system.

(b) Secondary systems:

1. Recurrently in the secondary leptome of the root and stem, forming continuous concentric systems. There are no transverse anastomoses between the several concentric systems, such as occur in a laticiferous plant, *Manihot glaziovii*, according to Calvert and Boodle (*l.c.*).

#### PRIMARY CANALS IN THE ROOT AND HYPOCOTYL.

These have their origin in the endodermis and are included within it, as shown for many Compositæ by Vuillemin, van Tieghem, Col (*l.c.*), and Holm (1908).

To be noted is a formation of a band of Caspary in the new walls arising in the cells destined to become a part of the canal. In the root there are two groups, one group of two to four (or occasionally six) canals opposite each primary phloem bundle (plate 36, fig. 1). While this grouping is generally true for the Tubulifloræ, the number of canals varies, *e.g.*, in

<sup>1</sup> For a summary of the knowledge of the resin or oil canals in the Compositæ up to 1903, see Col (1903). An excellent historical sketch of the development of our knowledge of organs of secretion of oil, resin, etc., is given by Tschirch (1906) at p. 1095.

<sup>2</sup> In the usual sense as employed by, *e.g.*, Vuillemin (1884b), and by Calvert and Boodle (1887).

<sup>3</sup> Vuillemin (1884b) properly pointed out the independence of the canals of the hypocotyl and epicotyl. He says: "les systèmes sécréteurs des deux membres ou des régions différentes de même membre sont toujours distinctes."

<sup>4</sup> As to origin.

*Silybum*. Col states that there are six in each group, and it appears from his account that the number of those which pass into the hypocotyl is scarcely reduced.<sup>1</sup> In *Parthenium argentatum*, however, the number of primary canals is usually not more than four; hence it appears that in the transition zone the number of canals may be doubled. The four primary canals of the hypocotyl pass into the petioles of the cotyledons in pairs, there to end blindly (plate 31, figs. 1 and 2). They do not reach as far as the blade.

The absence of canals in the blade of the cotyledons is to be noted. According to Vuillemin, the more numerous canals in the hypocotyl of *Calendula officinalis* pass (in part?) into the cotyledons, on which point Col takes issue. Col's figure of the seedling of this species shows groups of canals opposite four epicotyledonary bundles, and these he identifies with the hypocotyledonary canals, and shows none in association with the paired median-trace bundles of the cotyledons. The position in which Col's drawing shows the canals suggests that they may be the lower ends of the epicotyledonary canals. In many cases, indeed, the true hypocotyledonary canals may not follow the primary median bundles even into the petioles on the cotyledons, while in other cases they may. They may, therefore, end blindly in the hypocotyl, by a morphological recedence which Col has cleverly traced for the plant as a whole by his extended comparative study of numerous Compositæ. In *Parthenium argentatum* there are no other canals in the cotyledons (plate 34, figs. 4 to 6).

## PRIMARY CORTICAL CANALS.

### IN SECONDARY ROOTS.

Primary cortical canals in secondary roots and in those of higher orders arise *de novo* from the endodermis of the new member. This is brought about by the morphological independence of the endodermis in the roots of different order. Secondary roots are not infrequently triarch (plate 36, fig. 4), and have then three groups of canals, two to four in each group. In roots, either primary or of a higher order, which grow chiefly in length, the canals attain relatively large transverse dimensions, and, with a lacunation of the septæ between them, there arise columns of cells connecting the tangential walls (plate 36, fig. 3). The interpretation has been properly applied by Col (*l.c.*, p. 166) to similar appearances in *Solidago*. Col's observations do not, however, negative Vuillemin's previous conclusions, "dans les vieux rhizomes d'*Arnica montana*, etc.," as I point out elsewhere.

### IN THE EPICOTYL AND DEFINITIVE STEM.

As one ascends the axis the endodermis becomes, as is usually the case, a less definite structure. For this reason it becomes increasingly difficult to determine with precision the exact origin of the primary corti-

<sup>1</sup> Vuillemin (1884a) notes in *Silybum* a reduction in the number of endodermal root-canals by ending blindly, so that a reduced number pass through the hypocotyl into the cotyledons. The question naturally arises whether the reduction in number is not produced by coalescence, as in guayule.

cal canals. At the level at which the earliest canals appear, namely, immediately above the level of the cotyledonary node, the difficulty is not as great as higher up. Here the endodermis is evidently involved, and it seems conclusive that the whole of the canal structure is derived from it, though the cell lineage is not as evident even in a young condition as it is at higher levels in *Parthenium incanum*. This at any rate accords with previous observations,<sup>1</sup> and is without any doubt the case in those parts of the stem where the endodermis is regular enough to display its morphological relations. I therefore conclude that, were it possible to follow the development of the structure, it would be found, even in the higher parts of the stem in *Parthenium argentatum*, where the endodermis is quite ill-defined, to have originated in this.

The course of development is as follows: A tangential division takes place in one, or it may be two or three neighboring endodermal cells. In the cell destined to give rise to the canal a radial<sup>2</sup> division crosses the first wall so as to form four cells, realizing the "*division crucial*" of van Tieghem. Periclinal divisions, however, take place, cutting off special secretory cells, four in number, from a tier of supporting cells, while these suffer a still further subdivision. Two pairs arising from the inner two cells of the original four are cut off, and are, so to speak, discarded from the canal structure, as occurs also in the primary root-canals. Only the outer cells of the outer original two become divided, so that fourteen cells in all arise, of which four are the original secretory cells, six are the supporting cells, and four, or perhaps six, excluded—this in the mariola, *Parthenium incanum* (plate 37, fig. 8).

The canals of guayule (plate 37, figs. 1-5) bear sufficient resemblance to those of the mariola, so that it would be unsafe to deny their entirely endodermal origin. Secondary changes, by which the number of secretory cells as well as that of the supporting cells is multiplied, need not be described, as they consist only of repeated radial divisions and sometimes of tangential ones in the secreting cells.

These canals suffer more or less displacement (plate 37, fig. 3) according to circumstances, often sufficient to mask their origin. For this reason they have been alluded to as cortical by Ross (1908) and by Fron and François (1901), without raising the question as to their origin. This is, perhaps, the reason that, although Col (1903) asserts the endodermal origin of the cortical canals in the Tubulifloræ, his drawings sometimes fail to show clearly this derivation, as, e.g., in *Aster æstivalis*.

In *Anthemis mixta* and *Lasthenia glabrata*, however, the origin is clearly shown, and it seems that the canals are less elaborately organized than in *Parthenium* and suffer less displacement. My own effort has been to show conclusively the origin of these canals, with the result that the work, in part of Vuillemin, of van Tieghem, and of Col, is supported.

<sup>1</sup> Van Tieghem (1884) insists correctly upon the endodermal origin of the primary canals, but I am unable to recognize the distinction between canals "*bordés*" and "*non-bordés*," though, correlated with the more definite character of the endodermis in the roots, the canals are here more regular and somewhat simpler in their structure (but certainly not "*non-bordés*") than in the stem.

<sup>2</sup> With respect to the stem.



## TOPOGRAPHICAL RELATION OF CORTICAL CANALS.

The canals of endodermal origin, instead of taking a cortical position, may, in various plants, take a position within the pericycle alternating with the bundles, or opposite the bundles between the leptome and the endodermis. Holm finds such canals in *Ambrosia artemisiæfolia*, though such was supposed to be the case for *A. trifida* only (Vuillemin, van Tieghem). In *Eupatorium* (Holm, 1908), also, canals occur "outside the leptome." The displacement of the canals and accompanying cells of the endodermis to a position nearer the axis appears to have led Vuillemin to draw the conclusion that the endodermis of the stem is superposed on that of the hypocotyl, an inference which, as Dangeard (1889, p. 122) has said, needs confirmation. Vuillemin's figure (*l.c.*, p. 191) is susceptible of a different interpretation.

In the young epicotyledonary axis in *Parthenium incanum*, the canals of the cortex are more usually arranged in pairs, flanking the median leaf-traces. This is the permanent arrangement, as, *e.g.*, also in *Zinnia* (Vuillemin) and in *Olearia haasii* (Col, 1903). It comes about, therefore, that in the definitive stem of this plant the cortical canals are alternate in position with the bundles. In the guayule they are usually placed on the same radius with the bundles, and stand therefore opposite the leptome. Both of these arrangements occur in various Compositæ.<sup>1</sup>

The transition from an alternating position of the canals with respect to the bundles in the epicotyl to the radially opposite position presents an ontogenetic summary of these two conditions characterizing various Compositæ in which one or the other arrangement occurs. It may be added, however, that the position opposite the bundle in guayule is not invariable; exceptionally, canals occur opposite medullary rays. This is true of both primary and secondary cortical canals, though Ross states the contrary.

## ANASTOMOSIS.

Anastomosis and branching frequently occur between the canals of the primary cortical system. The four earliest-formed epicotyledonary canals, which arise in pairs associated with the first and second primordial leaf-traces, are connected, each with the other canal of each pair, by a transverse meatus, which lies above the level at which the lateral cotyledonary traces pass out from the axis. This transverse meatus is a prominent feature of the epicotyl, and is frequently the starting-point of several, usually four, canals. Anastomoses in the definitive stem are usually to be found at the nodes, and in stems with very short internodes they are frequently quite numerous. For this reason, in part, the number of primary cortical canals seen in a transverse section varies, as stated by Ross (1908). As the stem thickens (aside from secondary changes) the number of canals increases, so that from 5 to 20, approximately, may be seen (plate 36, fig. 5).

<sup>1</sup> There are very few cortical canals in *Parthenium lyratum* and in *P. hysterophorus*, and they occur on one or both sides of a bundle, but not opposite to it. Neither do they stand opposite a medullary ray, strictly speaking, though this appears to be the case in *P. incanum*. In *P. arctium* Bartlett they are numerous and alternate with the bundles.

## MEDULLARY CANALS.

## IN THE EPICOTYL.

All medullary canals are protogenic. Secondary ones do not occur. The typical number of canals is not established for ten or more internodes, this probably being variable. In field seedlings, or ones of slow growth, the distance from the cotyledonary to the tenth node is very short, and the particular behavior of the canals is difficult to determine. Etiolated seedlings, therefore, throw more light on the matter, though it can not be asserted that the behavior in such is always normal, *e.g.*, when the canals end blindly above, as they have been observed to do, instead of continuing to the apex of the stem. These short canals may, perhaps, be regarded as "poches sécréteurs"—the pockets in which Col sees reduced canals. The following notes, based upon a series of sections made of a seedling about 10 cm. tall, with 16 nodes, show that the definitive condition is established only at length, even the sixteenth node being sometimes reached before the full complement of canals occurs.

No canals below the fifth node.

At fifth node, one canal passing into bud.

Fifth internode, lower part, no canals; upper part, four canals.

Sixth node, one of these into bud. One branches, making four entering lower part of sixth internode.

Upper part of sixth internode, two canals; higher up, three, one sending a branch to bud of the seventh node.

Seventh node. At this level two more canals, making five to enter the

Seventh internode, in which one ends, leaving four in middle part.

Eighth node, four canals, of which one branches into bud.

Eighth internode, two canals in middle part. One branches, making three to the

Ninth node, at which the bud receives a branch.

Tenth node, four, one branching to bud. All but one end blindly, so that the

Tenth internode receives only one canal. Two more arise, making three for the

Eleventh node. One passes without branching into the bud, leaving two to enter the

Eleventh internode. One of these ends, so that one canal reaches the Twelfth node, at which one more arises by branching, and enters the bud.

Twelfth internode receives one, which ends blindly on reaching the Thirteenth node, where a new one arises and passes into the bud.

Thirteenth internode has no canals in the lower part.

Fourteenth node, one canal arises and passes into the bud.

Fifteenth and sixteenth internodes, two canals in each.

Despite the irregularity in numbers, and also in position, it is clear that the canals in the pith have peculiar relations with the nodes. When one arises it does so in connection with the development of an axillary bud, and either enters it or sends a branch to it. This is to be inferred also

from the regular occurrence of live canals, the primary number in the growing stem apex. In seedlings with short internodes the canals appear, of course, nearer the hypocotyl. In a field seedling 3 cm. tall, with two dozen or more nodes, I found one canal at 5 mm. above the hypocotyl. The next section cut had one. Similarly in an irrigated seedling with short internodes.

The absence of pith-canals in the epicotyl suggests a primitive alliance with those tubuliflorous forms in which canals are entirely absent from the pith.

#### IN THE DEFINITIVE STEM.

At the growing apex within 0.5 mm. one finds a strictly primary arrangement of these canals. There are five, one opposite each orthostichy.<sup>1</sup> In a slowly growing stem, however, in which the nodes are crowded upon each other, through frequent branching and anastomosis, the number seen will vary usually between three and six. The union and separation of the canals is associated with the formation of large lacunæ giving off large passages of irregular shape, but on the whole running longitudinally. In a single section, therefore, one may count as many as a dozen canals, and nearby as few as three or four. In rapidly growing shoots the anastomoses and branches are not so apparent, though they occur here also. From the canal nearest to it each bud receives normally a single branch, which, itself branching after entering the bud, increases till the complement is reached. Pith-canals do not enter the leaf.

#### TOPOGRAPHIC RELATIONS OF MEDULLARY CANALS.

Although the primary number of pith-canals is more or less masked by branching and anastomosis, as already mentioned, a study of the ontogeny of the stem can not fail to show that five is the primary number (plate 38, fig. 1), and further, that they arise in the same order as the leaves and, therefore, buds. These relations are seen best in growing tips of stems of not too slow growth, or in seedlings, just above the levels at which the pith-canals first come in. It is also evident from the positions taken by the solitary canals which appear in the epicotyl before the full complement is established.

The very frequent anastomosis and divarication, coupled with the transverse expansion of the canals, give rise to a great many columnar, trichome-like structures, already alluded to. They lie approximately in radial planes, and can be explained only as imperforate longitudinal septæ (plate 32, figs. 1, 6).

In older stems the breaking down of the pith results in the opening of the resin-canals, except when plugged by pseudotyloses. There results a downward filtration of resin which finds its way into the central zones of the old wood. This often becomes richly impregnated with resin, though primarily it contains none at all. In this way the resin-content of old wood, shown by chemical methods, is to be accounted for (Lloyd, 1909).

<sup>1</sup> In the pith of *Cynara carduncula* (Col, 1903) 5 to 10 canals occur; in *Parthenium hysterophorus* I count about 20; in *P. lyratum* about 12.



## THE CANALS IN THE LEAF.

Since the canals in the leaves are related only to the primary cortical system, this relation will now be taken up.

## EARLY FOLIAGE LEAVES.

The above-mentioned pair of primary cortical canals which enter the petioles of the earlier leaves end blindly at different levels in the petioles and in the leaf-blade<sup>1</sup> (plate 38, figs. 3 to 9). The marginal leaf-traces enter the petiole unaccompanied by canals, but arise *de novo* in the petiole dorsal to the lateral traces. There they follow into the leaf-blade, and branch, constituting a latero-dorsal system. The dorsal system may be entirely absent from the blade (plate 38, fig. 5). There is also a ventral system composed of three canals, one opposite each of three prominent bundles, namely, the median and two lateral. These arise independently and *de novo*, that opposite the median trace in the petiole, and those opposite the lateral ones, in the blade. They originate analogously with the pith-canals, independently of the endodermis<sup>2</sup> (plate 37, figs. 6, 7).

## THE LATER LEAVES.

The later leaves, in which their definitive character is assumed, receive usually three to five (occasionally six or seven) cortical canals from the stem, one with the median and two with each of the stronger lateral traces (plate 38, figs. 2, 10 to 18). These canals, which enter the blade, follow the traces which constitute its prominent veins. The lateral canals may branch, usually not more than once. Thus the dorsal system of canals has, at most, usually not more than five ducts. The median canal follows the midrib to the apex of the leaf. The lateral ends some distance from the apex. The ventral system arises *de novo* in the petiole as three to five independent ducts (plate 38, figs. 10 to 13), the median arising first. The lateral canals follow the main limbs of the lateral traces and give off branches to veins of a higher order, until, in a transverse section, there may be five or more on each half of the blade. It is thus seen that the ventral system is peculiar to the leaf and is more extensive than the dorsal system. The canals anastomose in the upper part of the blade and follow the veins.

## PRIMARY CANALS IN BRANCHES.

The primary system of cortical canals in a branch is derived from two canals on either side of the appropriate leaf-trace. At the level at which the bud appears, the adjacent canals in the chief stem enlarge radially and send

<sup>1</sup> The behavior described is not invariable. One case was found in which only one branch of the canal anastomosis entered the first leaf, while the second leaf was normal, having two canals. The third foliage leaf in this plant also had but one canal. One instance of a leaf at about the twentieth node had two canals. This condition offers an analogy to that in the cotyledons, which may be held, though only tentatively, as speaking for the more primitive character of the double arrangement.

<sup>2</sup> It is worth noting here that there is a single ventral canal opposite the mid-vein in the cotyledon of the common sunflower, *Helianthus annuus*.

off a number of branches which distribute themselves in the cortex of the bud. As already said, generally a single branch from the pith-canal opposite the bud enters and branches to produce the complement of canals (plate 39, figs. 1 and 7).

## SECONDARY CANALS IN ROOT, HYPOCOTYL, AND STEM.

These arise, as described by Ross, from special leptome parenchyma<sup>1</sup> derived directly from the cambium, and quite in the same way in all parts of the plant. They are at first flattened radially, opening out later to become rounded or even circular in transverse section, and finally becoming again flattened and secondarily distended, in company with the growing (secondary) cortex (plate 22, fig. 13). These canals constitute concentric branching and anastomosing systems, each succeeding zone being a system separate from all the others. Their appearance in tangential sections (plate 39, fig. 8) recalls the figure published by Tschirsch (1906, p. 1193) of the canals in wound-tissue in *Larix*.

## CANALS IN THE PEDUNCLE.

It has already been pointed out that the inflorescence is terminal; the peduncle is therefore the morphological chief shoot. I have shown that when an axillary bud develops it usually receives one canal from the pith (plate 39, fig. 1). The last bud formed on the chief shoot which ends in a peduncle, however, receives *all of the canals from the pith*, these being diverted *en masse*. The peduncle, therefore, contains no medullary canals (plate 39, figs. 2, 3). Primary cortical canals alone occur, there being but very little secondary thickening.

Exceedingly interesting relations in this regard are displayed by rapidly grown plants (plate 39, figs. 4 to 7). In another chapter two types of guayule have been described, in one of which the sharp delimitation between peduncle and foliage stem is not present. When guayule is irrigated there frequently results, associated with rapid growth, a tendency of the relatively chief shoot to run out into inflorescence,<sup>2</sup> when otherwise there would be a sharp transition from stem to peduncle, and the upper axillary bud would develop strongly. When the morphological transition is gradual, there is also a correlated anatomical transition, which the long internodes make it possible to analyze. In a specimen examined, as in the normal condition, the peduncle has no pith-canals, but the first internode below this has, instead of five, only two, which pass into the uppermost axillary bud.

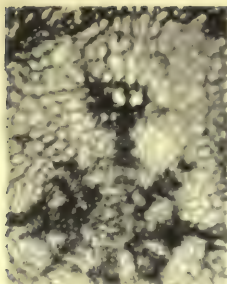
The sector of the stem under the peduncle contains much more stereome, and the two canals are confined to the sector beneath the axillary bud, while from the basal part of the internode they are absent! Their orientation above is such as to bring them opposite the first and second leaves of the axillary bud; they are, therefore, the canals which give branches to the first two axillary buds of the branch.

The axillary bud of the second node below the peduncle receives from the stem one canal only of four which are to be found in the internode be-

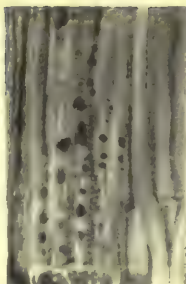
<sup>1</sup> Secondary leptome-canals have been described in *Centrophyllum lanatum* (Col, l.c.).

<sup>2</sup> Simulating the normal shoot in *P. incanum* (mariola).

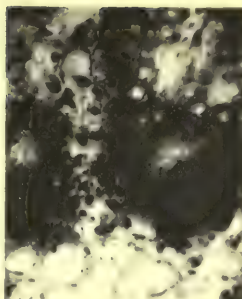




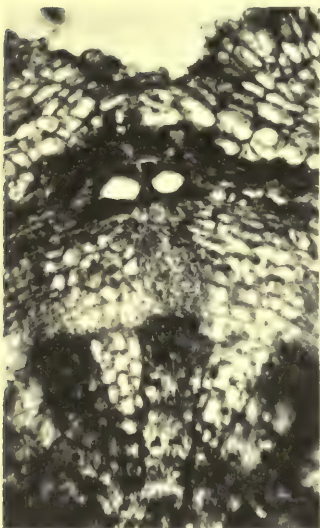
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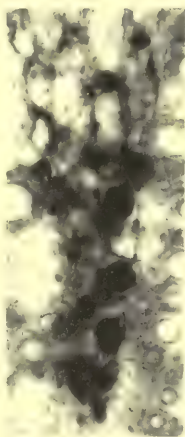
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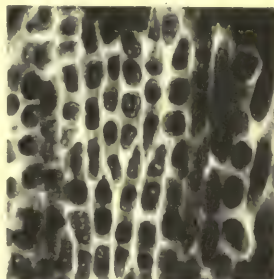
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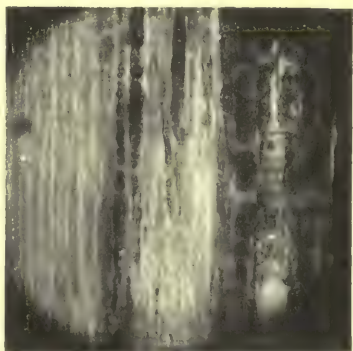
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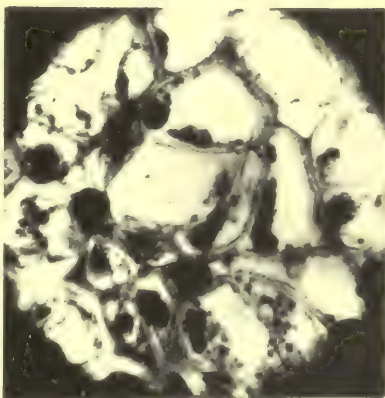
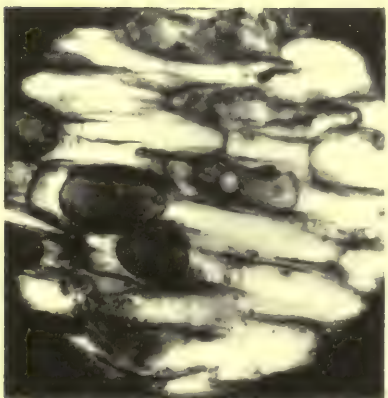
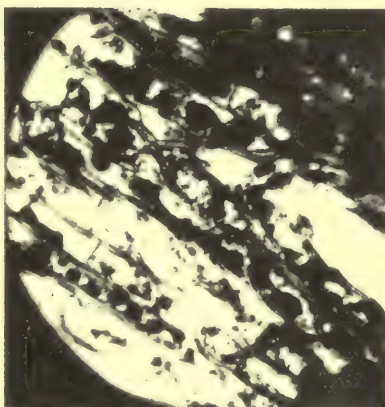
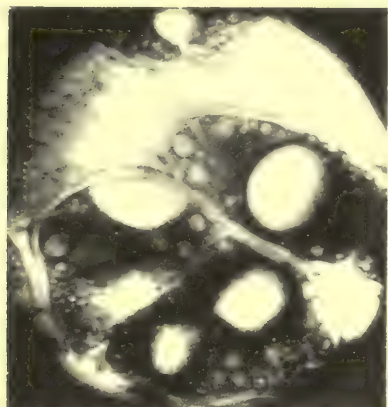
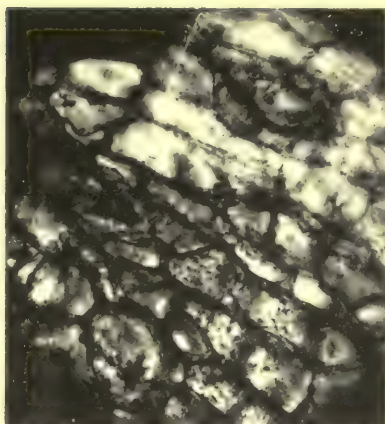
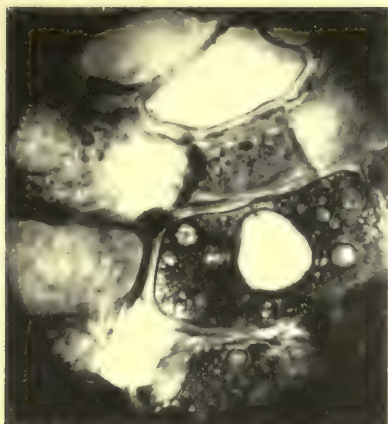
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1. Rubber in canal cells, nearby cortex and inner ray cells. Root 1.2 mm. diam.
2. Older root. More rubber in rays.
3. Root 2 mm. diam.
4. Parenchyma ray from fig. 2.
5. Upper part of hypocotyl, same age as fig. 1.

6. Longitudinal section through old wood.
7. Longitudinal section through mature leptome parenchyma, with a few parenchyma ray cells.
8. Leptome; elongated elements.
9. Companion cells and sieve tubes. No rubber in younger leptome on the left.







- 1, 2. Cortex, stem of field plant with maximum rubber content.  
3. Cortex of a 20-year-old stem.  
4. Root; rapidly grown seedling, two months old. Rubber in granules.  
5. Rubber in process of accumulation in an irrigated plant.  
6. Primary resin canal, root 1 mm. diam.





low the second node. The other three end blindly before they reach the node, so that the following internode has none, as above said. It is evident that we find here a sort of morphological indecision, as if the stem were trying to retain its stem character, and still being gradually overcome by the tendency toward changing into a peduncle. The same preparations show also the formation of chlorenchyma strips in the cortex of the peduncle sector, nearly down to the base of the first internode below the peduncle.

The axillary bud of the third node below the peduncle receives a single branch from one of five canals, the normal number, present in the internode below. Here, therefore, the complete stem structure is first met in our descent from the peduncle. It would be interesting to speculate on the internal causes which result in diverting the canals, *en masse*, from the chief shoot into an axillary bud.

### THE CANALS IN RETOÑOS.

New shoots which take their origin from roots have this peculiarity in common with the epicotyl, that they do not possess medullary canals till several internodes have developed. They are further peculiar in *lacking primary cortical canals* near their bases. A retoño 23 mm. long was examined and measured. A section near the root at the level of emergence showed neither pith nor cortical canals. At 5 mm. above it five cortical canals were found. At 10 mm. there were three medullary canals, and at 15 mm. five of these, so that at the level of 15 mm. the definitive structure had been attained.

In another specimen 25 mm. long, collected September 8, 1908, only one medullary was found at the level of 18 mm., and four at 21 mm. In still another, one canal was found at 15 mm.

An examination of a full series of transverse sections through succeeding nodes and internodes discovers an important relation of the pith-canals to branches, in general harmony with the facts cited immediately above. The material thus studied was a retoño several centimeters long which developed in 1908. The first leaf and its axillary bud were developed at the height of 20 mm. The internode between the mother-root and this node had no pith-canal. At the first node a single canal appeared just below the level of the bud, and entered this. The succeeding two internodes (second and third) were also devoid of canals, though at each of the corresponding nodes a single canal originated in the pith and passed into the axillary bud. At the third node, however, the canal branched, one limb passing up into the fourth internode, in the upper part of which two other canals appeared. One of these three sent a branch to the bud of the fourth node, and one ended blindly, leaving two passing into the fifth internode. At the fifth node one of these sent two branches into the bud, two canals passing into the sixth internode. At the sixth node both of these branched, one branch going into the bud and three upward into the seventh internode. At the seventh node all three branched, one of these going into the bud, leaving the full complement of five canals for the succeeding internode, the eighth. The youngest canal always stands opposite the youngest bud.

## THE CONTENTS OF THE CANALS ; THEIR ORIGIN.

The very small size of the primary canals in the root and hypocotyl makes it very difficult to determine the nature of their contents. The canals elsewhere are known to contain resin which, upon wounding, exudes as tears, which fall to the ground and harden slowly as pale yellow, limpid masses. The origin of this secretion is of special interest here. There is no doubt that the resin is confined to the canals, and there is no evidence that the resin occurs in the protoplasm of the wall-cells of the canal, which have been spoken of as secretory. Treatment with alcohol or with acetone leaves the cell-contents quite unchanged to all appearance, though subsequent staining with alkanet discloses, when this is originally the case, a substance which may be dissolved out by means of xylol or other appropriate solvent, namely, rubber. My own observations, therefore, give support to the general view, advanced by Tschirch, that the resin is to be accounted for by chemical activity in the outer part of the cell-walls facing the meatus. It is not a direct result of protoplasmic activity, but of enzymatic activity in the cell-wall itself.<sup>1</sup> It is worthy of remark that the wall (secretory) cells of the resin-canals have the two-fold function of secreting rubber (in common with the ground-tissue) within the protoplasm and resin without.

I have, however, attained no success in demonstrating a mucilaginous or gummy lining to the meatus, such as is described by Tschirch (1906, p. 1119) in many plants, to which he ascribes the origin of resin formation. But Tschirch himself confesses to a similar difficulty in studying, among others, the *Compositæ*.

The distribution of starch in the cortex and its apparent connection with the secretion of resin have been elsewhere noted. The presence of tannin in the conjunctiva of the young stem, especially associated with the chloroplasts, is to be noted, and recalls Tschirch's hypothesis of the origin of resin from tannin. The number of *Compositæ* which contain tannin is small, relatively to the size of the group, judging from the list given by Dekker (1906).

## THE RÔLE OF RESIN.

It has often been pointed out<sup>2</sup> that resins and ethereal oils stand in relation to climatic conditions, especially those of the desert. The frequent occurrence of resin in desert plants is a matter of general observation, but its function is still a matter of speculation. Tschirch rightly lays stress upon the occurrence of secretion-containing structures near the apex of the young parts as of significance, and this has been pointed out for the guayule. The evidence regarding the relation of resin to rubber leads us nowhere, and no evidence is yet forthcoming as to the real rôle of resin.

<sup>1</sup> Tschirch, A. *Die Chemie und Biologie der pflanzlichen Sekrete*. Leipzig, 1908.

<sup>2</sup> *e.g.*, Tschirch, 1908, pp. 8-9.

## RESIN-CONTENT OF GUAYULE BY ANALYSIS.

The percentage of resin in the branches and twigs of field plants, according to figures obtained by Whittelsey (in manuscript), is between about 10 per cent for the smaller and about 17 per cent for the larger branches. The amount probably varies according to the structure, and this with the rate of growth of the parts. For irrigated plants the following figures were obtained. The material was the same as that referred to in table 53.

TABLE 51.

Parts.	Percentage of resin.
I. Stump.....	2.46
IIa. Wood of 1907 growth.....	1.36
IIb. Cortex of this.....	4.06
III. Growths of 1908 intact.....	7.56
IV. New growth of 1909 with leaves.....	2.70
V. Roots.....	10.80

Aside from possible errors, it seems that, bulk for bulk, the irrigated plant contains less resin than the field plant. This is due in part to the larger relative volume of the wood cylinder. The reduction of the amount in older growths is due also in part to the radial compression of the resin-canals in irrigated plants, whereby their capacity is much reduced. The force of this explanation of the figures appears when we compare the percentage of resin in III above. When we introduce the rate of growth as a factor we must conclude that the total secretive activity is not reduced under irrigation, nor is the secretive activity of the resin-secreting cells lowered. The result, however, is had that in a given volume of cortex there is less resin in irrigated plants. In the pith, however, this does not hold, since the relative volume of the resin-canals under irrigation is as great or greater than in field plants. The reduced amount of resin of the cortex, volume for volume, appears, therefore, to be a secondary matter only, and bears, so far as we can see, no explanation in terms of adaptation.



## CHAPTER VII.

### THE ORIGIN AND OCCURRENCE OF RUBBER.<sup>1</sup>

Well-nigh nothing is known about the cytology of rubber-secreting cells. The great initial difficulties in the investigation have arisen from the fact that in most rubber-producing plants this material occurs in latex. In the guayule, as in a few other known plants, the rubber is laid down within certain cells, in a manner analogous to the formation of starch. Although the study of the early cytological activities which lead to the accumulation of rubber still presents great difficulties, since some of the agents used dissolve out the rubber, nevertheless it has been possible to determine the relation of growth and of some of the more important external conditions to rubber secretion. These results are important economically, since we are able to determine the time at which the maximum, or near the maximum, amount of rubber occurs, and during what period rubber is absent from the new tissues, and thus establish rules of procedure in the harvesting of the shrub.

### METHODS.

The solubility of rubber in xylol and the like prevents the use of paraffin. The preparations must therefore be studied in such a fashion that the rubber is intact. When present in large quantities it is easily recognized, after one has become acquainted with its appearance.<sup>2</sup> When in small quantities, however, it may easily be mistaken for droplets of oil or resin, or for protoplasmic or other granulations, and inasmuch as oils and resins as well as rubber are stained by alkanet, these substances, if present, must be removed by suitable solvents which will leave the rubber unaffected. For this purpose I have treated sections with high-grade and absolute alcohols, acetone, and potassium hydrate, applying alkanet both before and after. There remains the possibility that the substances which remain and which react to alkanet are not always rubber in its final form, but there can be little doubt that the materials which are referred to below are either rubber or are substances in the course of change into rubber. The evidence seems to indicate, however, that it is rubber which we are dealing with.

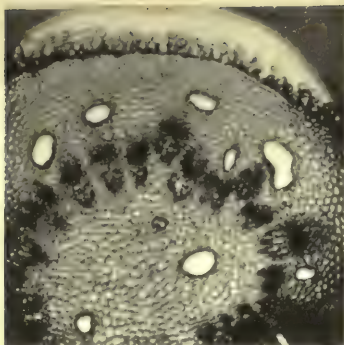
In seeking to determine with accuracy the facts of the distribution of rubber in the tissues, the accident of displacement of rubber in the act of sectioning must be properly guarded against. When rubber is present,

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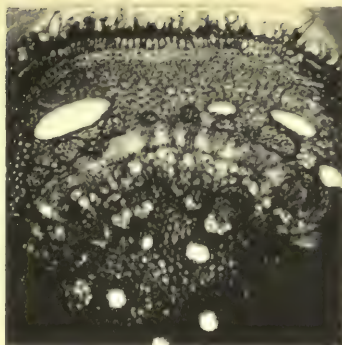
<sup>1</sup> The substance of this chapter was presented in a paper entitled "The responses of the guayule, *Parthenium argentatum* Gray, to irrigation," before the Botanical Society of America, Boston, December 1909.

<sup>2</sup> When in readily appreciable quantities, resin and rubber in the guayule may readily be distinguished by alkanet. Resin takes on a brilliant scarlet, while rubber has a purplish tinge, and is, to the naked eye, blood-red.

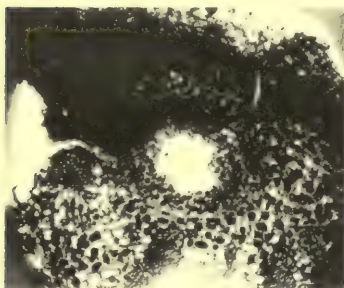
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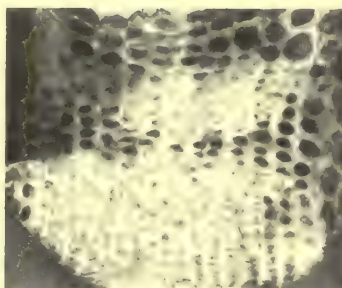
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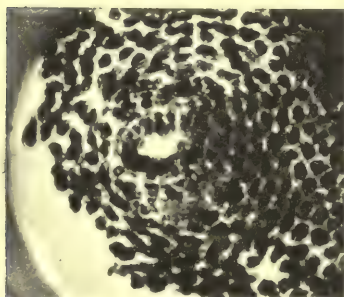
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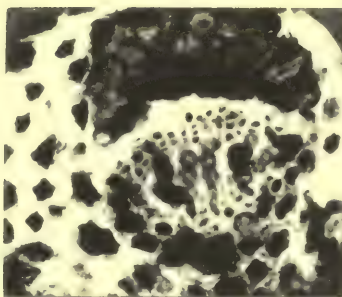
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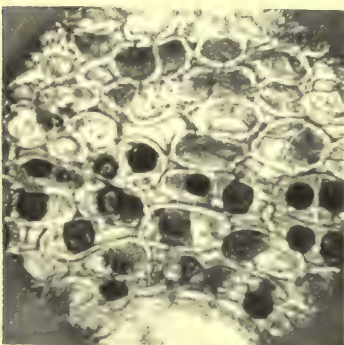
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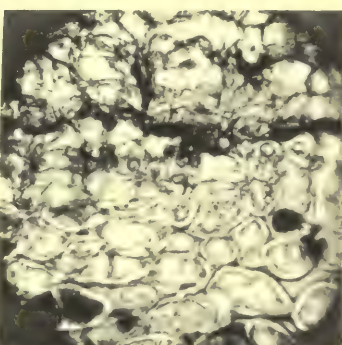
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7



8



1. Apex of terminal twig of 1908, field plant, July 22.
2. Near base of same.
3. Pseudo-tylose with rubber in the cells.
4. Leptome, field plant.

5. Pith of a field stem, 10 mm. diam.
6. An old leaf trace.
7. Outer cortex of a field stem.
8. Outer edge of cortex and inner zone of cork derived from collenchyma.





the contents of the cells ruptured during the sweep of the knife agglomerate and stick in irregular masses to the section. It is also to be suspected that particles of rubber displaced from one cell may remain attached to other cells in such a manner as to simulate an original position in them. This danger is greater where the particles are small, since with smaller size the chance against agglomeration is greater. With some experience, however, this general difficulty is reduced, so that, with proper observation, mistakes are easily avoided. The guiding principle of observation is simply to confine study to uninjured cells.

### GENERAL DISTRIBUTION OF RUBBER IN THE PLANT.

It has been known for some years<sup>1</sup> that the rubber in guayule occurs in the parenchyma "cells" of the stem and root; that is, in the pith, parenchyma rays, and cortex (the conjunctiva, in a word). These facts, though known to a few, were first clearly stated by Ross in 1908, according to whom rubber occurs in almost all the cells of the ground-tissue in root and stem; that is, in those of the pith, parenchyma-rays, primary cortex, and also in the wood-parenchyma. The leaves, he adds, contain little or none. While I have been able to confirm these conclusions in general, several additional details have come to light.

Rubber occurs invariably in all the cells of the resin-canals (plate 41, figs. 4-6). While I am unable to state positively that it occurs here earlier than elsewhere, it certainly is secreted most rapidly. There is, however, evidence that the former statement is true.

In the primary hadrome parenchyma rubber does not occur early. In the preparations from which the photographs on plate 42 (figs. 1 and 2) were taken, there was no trace of rubber. There can be no doubt, however, that rubber is secreted by some or all of these cells later on, as they are replete after some secondary thickening has occurred in the leaf-trace, which, of course, suffers no secondary change<sup>2</sup> (plate 42, fig. 6). The cells of uniseriate parenchyma rays, in consonance with other parenchyma-ray cells, contain rubber.

In the primary leptome, under the conditions noted for the primary hadrome in the preceding paragraph, rubber occurs at least in the fiber-cells and in the parenchyma (plate 42, fig. 6). This takes place after the abscission of the corresponding leaf. In secondary leptome I have seen small amounts in mature fiber-cells, just before sclerosis sets in. Occurrence of rubber in these elements appears, therefore, to be a function of age. It is secreted normally in leptome-parenchyma, and at the same time is in adjacent parenchyma-ray cells (plate 42, fig. 4).

In the secondary leptome rubber may also be seen in all the elements of the sieve-tissue (plate 40, figs. 8, 9). It is true that the very narrow

<sup>1</sup> Fron and François, 1901.

<sup>2</sup> The parenchyma of the secondary hadrome is rather scanty and of small elements. They do not secrete rubber as early as the medullary-ray cells in the same zone, but ultimately do so. The rubber may best be seen in longitudinal sections, treated with boiling 10 per cent caustic potash and stained with alkanet. The rubber then appears as small series of globules. The wood may also be macerated by means of Schultz's medium, and later stained.

elements contain very little, but this amount may be clearly demonstrated in longitudinal sections treated as above described.

In the cork-cells rubber occurs in a secondary condition as small droplets, derived by the breaking up (possibly an emulsification) of the compact masses in the outer cortex. These droplets are larger in cork-cells on either side of collenchymatic zones which are remnants of the periclinal walls of collenchyma (plate 42, fig. 8).

Rubber is secreted in the parenchyma of the pseudotylloses (plate 42, fig. 3), quite as in the adjacent cells.

In the leaf the amount of rubber, though always small, is in proportion to its age. In the oldest leaf I have observed, rubber occurs in droplets in the outermost palisade-cells of both surfaces, and less conspicuously in the subjacent, but usually in no other chlorenchyma cells (plate 43, fig. 5). It may occur only in the ventral palisade in younger leaves. In very minute droplets it is to be found also in the collenchyma and endodermis of the midvein and in nearly all of the non-chlorophyllous cells in the region about it, and in the leptome, both in the companion and sieve cells. Curiously enough, it is not to be found in the secreting-cells of the resin-canals, though, on the other hand, it is in small but conspicuous quantities in the subjacent cells. A minute amount occurs in the epidermis, especially near the midvein, and in the non-chlorophyllous cells near the smaller veins. The maximum quantity, negligible from the economic point of view, occurs in the oldest leaves which have passed through a drought period. The material which gave these results was collected in the spring of 1909 before the summer rain of that year.

In material collected from irrigated plants at Cedros in April 1909 rubber may be detected in exceedingly minute quantities in the basal part of the leaf only. A single minute droplet—not more than one-fourth the diameter of those seen in the field plant—may be seen in each outermost palisade-cell of the upper (ventral) surface. They are a trifle larger near the midvein. In the non-chlorophyllous tissue near this the rubber may also be detected in still more minute quantities.

Since within the periphery of the wood cylinder only the conjunctiva and a small amount of wood-parenchyma contain rubber, and since in older wood the medullary rays (in part) and the pith and its canals are dead and disintegrated, the wood cylinder contains less rubber than the cortical tissues, but it is also less resinous in its primary condition. Recent work by Whittelsey (1909), however, indicates that in stems of an advanced age, at any rate, the amount of true rubber is practically reduced to *nil*, though in the young twigs the proportion of rubber within the periphery of the wood cylinder is large. We must conclude, therefore, that the rubber in the older wood undergoes chemical change, and is broken down into related materials. There is no doubt that some such change takes place also in the secondary cortical tissues cut out by the inner periderm, and this, as I have shown, is a considerable part of the volume of the "bark" in older stems.

## APPEARANCE OF RUBBER IN RICHLY LOADED TISSUES.

A section taken through any young stem of a field plant after some period of drought will give a typical appearance (plate 42, fig. 7). All the cells of the conjunctiva appear to be filled with a gray substance. A good deal of it will have been swept out of ruptured cells by the knife-edge and agglomerated, the resulting masses having irregularly rounded outlines, with strands stretching here and there, still attached to the tissue. These masses, seen obscuring the pith to some extent in plate 43, fig. 2, and the dense cell-contents stain deeply with alkanet, the stain being more brilliant if the sections have been previously boiled in a 10 per cent solution of caustic potash. If the sections have not been acted on by alcohol or potash drops of yellow resin will be seen in the resin-canals, but nowhere else, except accidentally.

Closer examination of the rubber within the cells shows that the mass is not homogeneous, and does not entirely fill the cavity. It may form a heavy layer about the wall, leaving a more or less irregular space within, or, if apparently filling the entire cell, it will contain numerous spherical spaces (plate 41, figs. 1, 2). Sections which have lain in glycerin may show the masses to be contracted, owing to a plasmolytic action upon them, from which it is to be inferred that they have a considerable water-content, held within the vacuoles, in part at least (plate 41, fig. 3). The rubber may also accumulate as a round drop within the vacuole of the cell (plate 42, fig. 7), its size depending upon the age of the cell. Plasmolysis shows further that all the parenchyma cells are not equally densely filled, though of the same age. This is often conspicuously the case when the cells of the cortex and those of the adjacent parenchyma rays are compared. In the cortical cells the rubber forms a dense rounded drop (plate 42, fig. 7), while the cytoplasm may be seen between it and the cell wall. In parenchyma-ray cells the rubber mass is frequently irregular, full of irregular vacuoles, and the cytoplasm appears usually to have shrunk away with it. In the parenchyma-ray cells in some preparations it is quite as regular as in the adjacent cortical cells, but appears to be more dense, owing to a very much larger number of minute spaces. This difference, in one form or the other, is quite constant, and seems to indicate that the rubber-content of the cortical cells is higher than that of the adjacent parenchyma-ray cells.

Cortex which has been cut out *en masse* by inner periderm also contains rubber. In the cells of this tissue it has a still different appearance, being segregated into droplets of various sizes, in a fashion to suggest the analogous appearance of dead protoplasm. In newly formed cork-cells proper, just outside of the periderm, a different behavior is seen.

## BEHAVIOR OF PERIDERMAL DIVISIONS TOWARD RUBBER.

Since the secondary cortical cells in field plants contain a large amount of rubber in the condition described, the fact that the cork-cells immediately outside of the actively dividing suberogenous cells may contain no rubber at all, or only occasionally a small amount, calls for explanation. The suberized walls of the cork take up alkanet readily, so that, after



treatment with that reagent, the contrast between the rubber-containing cells of the cortex and the empty nearby cork-cells is very clear and striking. Inasmuch as the peridermal divisions, though several times repeated in the same mother-cell, finally involve a considerable depth of tissue, and as the rubber can not travel from cell to cell as such, we must conclude either that the rubber is translocated, which is unlikely, or that it disintegrates. In support of the latter conclusion we note the following ocular evidence:

1. When the first cork-cambium division takes place the partition passes through the rubber-content, whereby the two daughter-cells each receive a share (plate 31, fig. 14). From the outer cell, which becomes suberized, the rubber disappears.

2. This disappearance is gradual. The rubber may first break up into droplets, which become fewer in number till, in the second series of cork-cells, scarcely any evidence of its former presence remains, or it may become shrunken in appearance. During this time the rubber, if it still is such, reacts less characteristically to alkanet, and takes on a dirty bluish tint. In one young root, however, I observed droplets of rubber giving the characteristic stain, out several cells distant in the cork. The explanation may be that after the death of the protoplasm the oxidizing enzymes present hasten the disintegration. This may be less rapid in the root, though it is difficult to say why. The mere contact with the air would seem an insufficient explanation, since disintegration of the rubber in cortex cut out bodily by inner periderm is very slow.

#### THE DEVELOPMENT OF RUBBER IN THE CELL.

All that we are able to do microscopically in regard to the method of origin of rubber in the cell is to detect its first appearance and the subsequent accumulation, and we are therefore precisely in the position of the poet who said of a matter usually regarded as far removed from the realm of science,

"Sie kommt, und sie ist da."

We are unable to say at this point whether the origin is associated with special organs as plastids or not, though my observations up to the present indicate that there are no such organs.

The relation of nuclear activity in general to secretion is well known. The rubber in the palisade-cells of the leaf appears first in all cases in contact with the nuclear membrane, and for this reason does not take the form of spherical but of concavo-convex droplets, seen in plate 43, fig. 5. Elsewhere the earliest appearance is as very minute, well-nigh invisible droplets (plate 41, fig. 4), scattered in the protoplasm. They grow in size and increase in numbers until the protoplasm is loaded sufficiently to render it exceedingly frothy in appearance (plate 41, fig. 5). These droplets may travel toward the interior of the cell and be extruded into the vacuole, where they run together to form a larger droplet or a more or less irregular mass. This is not homogeneous, as might be supposed, but is vacuolated, sometimes so much so that it is quite alveolar in structure (plate 41, fig. 1), sometimes less so, the vacuoles being widely scat-

tered. That these vacuoles contain various substances in solution in the inclosed water can not be doubted, and it seems likely that among these are enzymes<sup>1</sup> which may act upon the rubber after extraction by the mechanical processes in vogue. It also seems likely that the protoplasm of the cells becomes intermingled with the rubber during extraction, rendering it more or less albuminous and liable to give off the products of the decay.

## CENTERS OF SECRETION.

### THE ROOT.

With certain exceptions, the secretion of rubber both in the stem and the root, including the hypocotyl, appears to proceed from definite centers. This is exemplified with especial clearness in the root, where, in the cortex, the secreting-cells of the resin-canals<sup>2</sup> are the first to show the presence of granules of rubber (plate 41, fig. 6). It is argued that secretion actually begins earlier in these cells because the surrounding cortical cells, primary on the outside, secondary on the inside, contain, at an early stage of secretion, less and less rubber, as one proceeds farther from the canals. The figures of plate 40 illustrate this advance in secretion, the beginning of which is seen in a young stage in the development of the root (plate 23, figs. 3, 7; plate 40, fig. 1). If the rate of growth has not been too rapid, so that a part of the primary cortex has had the necessary time to secrete rubber before being cast off, the activity of secretion is seen to be taken up successively by the cells further removed, until the whole tissue becomes loaded (plate 40, figs. 2, 3). The greater amount of rubber, however, is evidently held by the cells nearer the resin-canals. In the hypocotyl the same physiological relations hold.

The secretive activity of the secondary cortex is taken up, aside from those cells in the neighborhood of the canals, by successive layers of cells, beginning on the outside. With the appearance of the secondary resin-canals, however, a superior activity in rubber secretion in their secreting-cells is to be early noted.

On the other hand, simultaneously with the appearance of rubber in the primary canal-cells, it appears also in the innermost cells of the parenchyma rays, the function of secretion being taken up successively by the next outer cells, and so on. This is apparent in the figures (plate 40, figs. 1 to 4). If a period of rapid growth follows one of stasis, the newly formed parenchyma-ray tissues will show an entire absence of rubber (plate 40, fig. 3). When secretion again begins, it starts simultaneously in the outermost and innermost cells of the parenchyma ray.

### THE HYPOCOTYL.

In the hypocotyl a similar condition prevails, though here, as in the definitive stem, there is a pith. That is, the innermost parenchyma-ray cells assume secretive ability earlier than the pith-cells, which is not true for the definitive stem (plate 40, fig. 5).

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<sup>1</sup> The presence of oxidases in extracted rubber, both in latex rubbers (Spence, 1909) and in guayule rubber, is known.

<sup>2</sup> In view of the emphasis which has been placed by many writers on the endodermis as seat of high physiological activity, the beginning of the secretion of rubber in the resin-canal cells, which are constituents of the endodermis, is of very great interest.

## THE STEM.

In the stem, the first evidences of rubber are to be observed in the secreting-cells of the cortical and medullary canals simultaneously. The dark appearance of these cells in figure 1, plate 42, is due, in part, to their larger rubber-content, but in part to the denser protoplasm. The condition to be seen in these cells is represented by the camera drawing in plate 31, figs. 10 and 12. The section was taken toward the apex of a newly grown twig of a field plant, collected on July 22, 1908, and was then about six weeks old. In all the cells of the conjunctiva very minute granules of rubber could be seen, but not more in the cells near the canals than elsewhere. In the stem, therefore, secretion appears to begin first simultaneously in the canal-cells of the pith and cortex, and then in the conjunctiva. It is, however, quite readily determined that the physiological activity of the pith is greater than that of the cortex. In fig. 2, plate 42, is shown a section taken from the twig just mentioned, but near the base of the new growth. One or two peridermal divisions have ensued, while other secondary changes may be noted. The rubber-content of the pith-cells is obviously greater than that of the cortex in this section. Further, I have noted in irrigated plants that the amount of rubber is greater in the outer than in the inner cortical cells (plate 43, fig. 1). It seems, therefore, that the deportment of both root and stem is essentially the same and that the hypocotyl, though possessing a pith, behaves as the root.

During secondary thickening, as in the root, the secondary cortical canals exhibit early activity in rubber secretion, while this is taken up by the oldest parenchyma-ray cells first, simultaneously, therefore, at the inner and outer edges.

## THE LEAF.

In the leaf the earliest appearance of rubber is in the outer palisade in the ventral moiety. I found rubber in these cells only in old leaves of irrigated plants. The analogy with the condition described for the stem, in which superior activity is shown by the pith, is clear. But the failure of the leaf-canal cells to show greater activity than the neighboring conjunctiva detracts from the force of the comparison. The leaf observed by me to be most richly supplied with rubber contained a single drop-let, with a diameter about half the transverse diameter of the cells, in each palisade-cell toward the median vein. The amount of the rubber became less and less toward the margin. This was true also of the outer palisade of the dorsal (lower) surface, and in a less degree of the inner palisade.

Minute granules occurred also in all the non-chlorophyllous cells, mechanical and conjunctive, forming the midrib, excepting the vascular and sieve elements. It would seem, therefore, that, roughly speaking, the midvein is the center of rubber secretion, which proceeds through the lamina toward the margins; further, that activity is shown first by the outer palisade-cells, then by the inner, and first by the ventral and later by the dorsal. In this regard, as already said, the analogy to the stem is clear.



## RATE OF RUBBER SECRETION RELATIVE TO GROWTH.

The material which I have studied in order to determine the relation of growth to the rate of rubber secretion was collected during and following the growing-season of 1908, which began about June 1. Growth is rapid for the first part of the season, during which several centimeters of stem-length are attained and one to three flower-stalks are developed. A period follows in which there is little lengthening, and more or less secondary thickening occurs, according to the length of the period during which growth of any kind may take place. During the first part there is no evidence of secretion of rubber in the new parts; during the second, which began in 1908 in late July or August, there is a slight evidence of secretive activity as regards rubber, though the secretion of resin is synchronous with growth. The relation may best be expressed by saying that the secretion of rubber is a secondary physiological process, its rate of appearance being inversely to the rate of growth. The rate relation is brought out best by plants grown under experimental conditions, in which the more rapid growth is accompanied by a less rapid secretion of rubber. No exact quantitative statement can be made, since the conditions under which experimental plants have been grown have not been fully controlled. In studying material, I have tabulated numerous observations in field and irrigated seedlings, of various ages and at different periods of the year, and compared the rubber-content of the cells in all the tissues with that in irrigated seedlings. The same has been done for mature field and irrigated plants. For this purpose the material which has frequently been alluded to was at hand, viz, the branches and stocks of irrigated plants at Cedros (plate 4, fig. B) and at Caopas (plate 46, fig. B), both immediately at the close of growth-periods and after a period of drought. The attempt was made to grade the preparations on the rubber-content of the cells, and while this method of procedure has little to recommend it for more than approximate accuracy, it enables us to draw reasonable conclusions as to the rate of progress of secretion. My observations have been digested in the following notes, which will serve to present sufficient concrete evidence to support my conclusion.

1. At the close of the dry season (May 1908) all the cells of rubber-bearing tissues produced by growth during 1907, both in new shoots and in new tissues in older shoots in field plants, contained rubber in maximum quantities (plate 42, fig. 7).

2. The same may be said, generally, for the field seedlings. There is, however, evidence that in the cells of the pith near the top of the seedling the maximum content of rubber is not reached. Seedlings (plate 17, fig. A) of rapid growth in 1908 had not reached the maximum content (as shown both microscopically and by the analysis on p. 187) in April 1909. In the cells of the root it was more densely agglomerated than in the stem. Here the rubber had the same appearance as in irrigated plants. It was only partly agglomerated, and only partially filled the cells. It is quite probable that this condition occurs occasionally in mature plants in drier habitats after exceptional rainfall and regularly in moister conditions.

3. A medium-sized twig, grown in 1908, beginning about June 1, measuring 3.3 mm. in diameter at the base and 1.2 mm. at the tip, was

examined Aug. 14. At the base the rubber in the pith was finely granular, showing in addition a tendency to agglomeration (plate 42, fig. 2); in the extreme inner and outer cells of the parenchyma rays the rubber was very finely granular, while in the cells lying on either side of the cambium there was none or extremely little; in the primary cortex it was finely granular, but was in somewhat larger granules in the secondary cortex; large granules occurred in the younger resin-canal cells (in the secondary cortex) and agglomerated masses in the older canal cells (in primary cortex and pith). Near the apex of the stem the rubber was found only in extremely minute granules everywhere (plate 42, fig. 1) excepting in the resin-canal cells, where they were somewhat larger, but still small (plate 31, figs. 10 to 12).

4. A similar twig, examined Sept. 8, showed that the condition seen at the base in the twig described immediately above had advanced toward the apex about one-third the length of the twig. At the base the rubber had increased till it had become coarsely granular, except in the parenchyma-ray cells nearer the cambium, in which it was still finely granular. Five mm. from the apex there was still scarcely sufficient rubber to be observable, except in the resin-canal cells.

I was unable to obtain material during the succeeding few months, so was prevented from following the march of secretion after September 8. It is, however, clear that the rate of secretion is so slow, as compared with the rate of growth, that for at least four months after the beginning of the rainy season the new parts contain only very small quantities of rubber. From this time on the secretion of rubber probably proceeds more rapidly, but it is still to be determined when the maximum is reached. This is a point of very great importance.

5. Turning to irrigated plants, I need cite the evidence from only three examinations:

(a) A branch (plate 21, figs. A, B) of a Cedros plant (plates 4 and 17, fig. B) which began to grow in 1907 and was examined in August 1908. In examining the 1907 growth no rubber was detected in the pith, probably because the small amounts secreted in 1907 had disintegrated; the older cells (of 1907) in the parenchyma rays contained rubber in fine granules near the cortex; in the cortex and resin-canal cells there were coarse granules with more or less agglomeration. The new tissues of 1908 contained only very minute granules. In the 1908 growth, near the base, the rubber was visible in very fine granules, save in the primary cortex, where there was none; in the resin-canal cells coarse granules, these still larger in the pith-canals; midway between the base and apex there were very fine granules of rubber in the pith and parenchyma rays; the resin-canal cells had coarse or agglomerated granules; fine granules were visible in the secondary cortex, but none in the primary. Four centimeters from the apex, where the stem was still herbaceous, minute granules of rubber had appeared only in the pith and inner parenchyma-ray cells nearby; it was present in coarse granules in the resin-canal cells of the pith, and in fine granules in those of the cortex; the cortex itself contained none (plate 43, fig. 1).

(b) A branch from a single Cedros plant collected in April 1909 (plate 17, fig. B), after a prolonged drought extending with practically no inter-

ruption from August 1908. Rubber was found in dense rounded agglomerations throughout, but evidently not reaching a maximum content (plate 43, fig. 2).

(c) A branch from a plant grown at Caopas, from stocks transplanted by Don Teofilo Delgadillo about January 1908 and taken in October 1909. These had less irrigation than the above-mentioned Cedros plants. 1908 growth: the rubber was densely agglomerated in the whole of the conjunctiva (plate 43, figs. 3, 4), in amounts exceeding that in Cedros material (plate 43, fig. 2); the 1909 growth contained rubber in coarse granules more or less agglomerated throughout.

6. Irrigated seedlings of all ages up to five months were examined. Very young individuals were seen which contained no rubber at all. A five-months-old seedling (plate 20, fig. B) contained rubber in coarse granules throughout the conjunctiva, being in sufficient quantity in the secondary cortex to become agglomerated.

The method which was used in obtaining the foregoing data, despite its limitations, could doubtless be used by the grower of guayule, enabling him to follow the behavior of the plants under his charge. The evaluation of the evidence is somewhat difficult, but it could be mastered, as may be seen, I think, on examining plates 40 to 43. The final control must, however, be had by chemical analysis. Tables 52 to 54, which follow, contain a few results which comport with the evidence preceding.

#### RUBBER-CONTENT BY CHEMICAL METHODS.

The analysis of the guayule plant in order to determine its rubber and resin content presented unexpected difficulties, but the results attained, after these had been met, are undoubtedly more reliable than earlier analyses. I therefore adopt them as exposed in table 52 (Whittelsey, 1909, pp. 3, 5).

TABLE 52.—Percentage of rubber in various parts of guayule shrub. Field plants.

Parts.	Rubber.
	<i>per cent.</i>
Trunk bark.....	21.4
Root bark.....	19.5
Branches and leaves.....	9.7
Trunk wood.....	0.0
Root wood.....	2.0

“The percentage of pure rubber in the whole trunk is 9.9, the whole root 7.8, the branches and leaves 9.7, and in the whole plant 9.5, \* \* \* based on perfectly dry material. If ‘mill weight’ is taken as a basis, the percentage of pure rubber in the whole plant is 7.8.” This result is found to correspond very closely to factory experience and the more accurate published results, and we may therefore adopt it as exact enough for the present purpose.

The only figures available for irrigated plants are given in table 53 on the following page.



TABLE 53.—*Analysis of irrigated plant two years old from transplanted stocks, Cedros. Collected April 4, 1909. Plant weighing 4.5 pounds fresh.*

- (I) The original stump planted March 1907, divested of its subsequent growths. (II) The growth of 1907 separated into wood and cortex: the wood (IIa), the cortex (bark) (IIb). (III) The growths of 1908 intact, and therefore comprising both wood and cortex. (IV) The growth of 1909, consisting of short new twigs and their leaves, developed before the date of collection. (V) The lateral roots intact.

Number.	Rubber.	Number.	Rubber.
	<i>per cent.</i>		<i>per cent.</i>
I.....	3.55	III.....	3.30
IIa.....	0.80	IV.....	0.67
IIb.....	3.68	V.....	3.95

The method by which the above data were obtained was worked out by my former colleague, Dr. Whittelsey. The method was controlled by myself microscopically, and the material was found after treatment to have been thoroughly, though not quite entirely, extracted. The error from this source, as shown by this control, is, however, extremely small, and the figures may be accepted as practically correct.

For the purpose of appreciating the practical significance of the data, we may compare the percentage of rubber in the new growth intact. For field plants we have a 9.7 per cent rubber-content. In the twigs of the irrigated plants studied the amount is 3.3 per cent, namely, a little over one-third that of field plants. By comparing IIa and IIb, we note that this low percentage is due, as shown in Chapter V, to the low percentage of rubber in the wood and its relatively larger volume in irrigated plants. Moreover, the "branches and twigs" of Whittelsey's table can not be directly compared with those of III in my own, but rather with II and III taken together. If it were possible to compare the cortices alone we should find, in all probability, a percentage of about 4 per cent of rubber for irrigated plants against 15 to 20 per cent for field plants, so that for the new growths under irrigation from the transplanted stocks in question the amount of rubber formed by cortical tissues is about one-fourth to one-fifth of that formed in the corresponding tissues in the smaller branches and twigs of field plants. But the rate of growth under irrigation is such as to result in the production of a volume of cortical tissues, at the very least five times greater for the same length of time. This factor would be very much increased if field and irrigated seedlings were compared. The conclusion would therefore appear to be reached that the difficulty attached to the problem of cultivating guayule for the rubber is not that of obtaining rubber, but of properly handling the raw material so as to extract the rubber from the tissues.

In the first place, we have repeatedly noted the relatively large volume of the wood cylinder in irrigated plants, and its density. We have also seen that the branches are long and lithe. If this material is handled in its entirety, the volume of barren material which must be handled by machinery is considerably greater than in the case of field plants. The suggestion (Whittelsey, 1909, p. 6) that the cost of manufacture could be reduced by the use of decorticating machinery, as is done in the case of "grass rubber" (*Funtumia* spp.) in Africa, is still more pertinent for

irrigated shrub, and the character of the growth lends itself to this. This would seem to be necessary in the event that the relative amount of rubber in the cortex can not be raised above 3.5 to 4 per cent, not only because of this probable difficulty of agglomerating the more finely divided rubber, but because of the interference with this of the fragments of splintery wood, which will tend materially to obstruct agglomeration in any event.

In the second place, the individual masses of rubber in the irrigated plant are smaller and further away from each other than in field plants. Hence, as above said, it is more difficult to agglomerate the rubber. This is noted in trying to isolate the rubber from irrigated tissues by mastication, a process more difficult than for field plants. It may be found necessary to introduce a machine especially adapted to mastication of the material after passing through the pebble-mill, in which rollers with differential speeds will cause the massing of the minute particles of rubber. But the practical solution of such problems is not to be obtained merely by reasoning about them. The laboratory and factory are mutually of value, but the one does not always solve the difficulties of the other.

#### VARIATION IN RELATIVE AMOUNT OF RUBBER IN FIELD PLANTS.

I have already pointed out that rubber does not appear in newly formed tissues for some time after the cessation of growth; it may be for a period of some months. It therefore appears that the new growth of field plants taken at some periods of the year has a content and distribution of rubber similar to that in irrigated plants, aside from the relative bulk of the tissues themselves. To illustrate, I take the following analysis of seedlings, from Station 2, Quadrat 4 (plate 17, fig. A), collected April 1909, germinated in 1908 (table 54). The leaves and stems with tap-roots were analyzed separately.

TABLE 54.

	Rubber.
	<i>per cent.</i>
The leaves.....	1.21
The stem and tap-roots....	2.40

Of interest in this table are the rubber-content of the leaves taken separately and the low content of the stems and tap-roots. The leaves probably represent the usual condition, as they were old, fully matured leaves which had remained attached to the plants throughout a long drought period. The plants, however, were of rapid growth, indeed remarkably rapid for field plants, and the low rubber-content stands in relation to this. There is no doubt that this rubber-content is much lower than for seedlings of the same size of slow growth.

In this respect, therefore, there is no hard and fast difference as between field and irrigated plants, nor indeed is this the case for the relative volumes of the tissues themselves, as I have previously shown (p. 117). The response of the guayule under irrigation, therefore, is but an extreme expression of what occurs in nature, correlated with the climatic differences which obtain from year to year, and in different localities.

## RELATION OF RUBBER AND RESIN.

A notion has been widely entertained that the amount of rubber in the guayule plant is in some way related to the amount of resin. This naturally grew out of the fact that commercial rubbers always contain more or less resin, and that resin is abundant in the guayule. In the preparation of the commercial article from the guayule the resin becomes intermingled with the rubber to the amount of 20 per cent (Whittelsey, 1909). There appears, however, to be no adequate evidence in support of this notion, while on the other hand there is strong evidence to show that the physiological processes involved in the secretion of these two materials are quite distinct:

1. The canals which are laid down in the protogenic tissues become actively secreting as regards resin long before rubber appears at all. This is strikingly evident in irrigated plants, in which the amount of growth is very much in excess of that in field plants.

2. Resin is secreted in other *Compositæ* in which rubber does not occur. In the closely related mariola (*Parthenium incanum*) resin is abundant, while rubber is very meager in amount; and this is true of many others.

3. In irrigated plants the amount of resin is correlated with the anatomical conditions within the organism, while the secretion proper appears to be neither retarded nor advanced by the presence of water. Water, on the other hand, affects markedly, though probably indirectly, the rate of rubber secretion, which lags behind growth. But the lagging behind of rubber secretion is not in inverse relation to any possible increase which may be shown to occur in the secretion of resin.

4. The distribution of starch appears to be connected with the secretion of resin, as in other well-known instances (e.g., *Pinus*). The secretion of resin appears, as above pointed out, to be extra-protoplasmic, and in harmony with the view expressed by Tschirch, already alluded to.

5. Rubber, however, appears in the tissues independently of the distribution of starch referred to in (4) above. However, the starch found in the young tissues near the growing apex may serve as a source of material for the elaboration of rubber.

6. The appearance of rubber in the canal-cells might be cited to support the view under discussion, but for the fact that the rubber is merely accumulated in these cells and that this occurs later than the secretion of resin. Further, rubber occurs in other tissues, e.g., parenchyma rays, far removed from resin secretion. Resin in the canal-cells has not been demonstrated, but *in the meatus only*.

## THE SIGNIFICANCE OF RUBBER.

The inevitable question as to the use of rubber to such a plant as the guayule, subject as it is to the severe conditions of the desert, has been raised and must be met in some wise. I have already briefly discussed the matter (Lloyd, 1909) with but meager satisfaction, as will appear to those inclined to find a use for everything in animate nature. I can only repeat here what I have already said.



The most obvious suggestion relates to the conservation of water, and it seems quite possible that the rubber may act as a sort of blanket, reducing to some extent the passage of water to the outer zones of tissue and consequently to the outside of the plant, and as a storage material. The slower deposition of rubber in irrigated plants and its behavior in *Castilloa elastica* under similar circumstances lend a modicum of support to this view. Rubber, as is well known, will take up and retain a certain amount of water with considerable tenacity. One would be encouraged to hold this view if rapidly grown field seedlings with much less than the normal amount of rubber had not been known to pass successfully through a long period of drought, indeed much longer than usual. Further, mariola appears to be as well equipped for resisting drought as guayule, but contains a very small amount of rubber. The obvious objection that the mariola has some other means to the end would in this case, I believe, be difficult to demonstrate, and as difficult to refute. We are here in the field of teleological speculation.

Spence (1908), studying latex, found that this contains oxidases capable of acting upon caoutchouc, and argued that this material may therefore serve as a reserve food material.<sup>1</sup> Similar enzymes probably occur in the guayule, but it is safe to remark that in this plant, once the rubber is laid down, it is there to stay, as shown by its abjection in company with the bark-tissues. Even in the cells adjacent to the active cambium, or other physiologically active tissues, the amount is never reduced, while, if of use as a source of energy to the growing twigs, we should find some evidence, analogous to that seen in the starch-content of growing twigs, that there is translocation. But such evidence is quite lacking. Whatever may prove to be true of latex plants, therefore, there does not appear to be the slightest evidence that rubber is in any sense a food material in the guayule.

This view has recently (1909) been again brought into question by Spence:

The fact that the caoutchouc, or rubber, does not occur in any definite latex system in the guayule, but in the parenchymatic cells of the medullary rays and cortex, and further, that the amount of rubber from the dried plant varies considerably from one period of the year to the other \* \* \*, seems at once to suggest to my mind that the rubber must have an important function in metabolic processes. That the rubber is cast off partially and *in a modified form* in the bark, as Professor Lloyd has pointed out, does not in any way weaken the evidence of my theory, and from experiments which I have recently made I have found that young *Ficus elastica* trees, grown in an atmosphere and soil free from carbon dioxide, gradually drew upon their milk, which became nothing more than water after a few weeks' time.<sup>2</sup> In any case \* \* \* the guayule plant shows very clearly that we can hardly retain the theory that the latex merely affords protection to the plant against internal injury and moisture in time of drought; in guayule there is no secretion on injuring the plant, and no reserve water-supply, though the rubber is there all the time. \* \* \*<sup>3</sup>

<sup>1</sup> See also Cook, 1903.

<sup>2</sup> There has been a long controversy on the function of latex, for an account of which see Tschirch, 1906.

<sup>3</sup> The quotation was printed in the past tense and third person. I have made it into the first person, present. The italics are Spence's. (Lloyd, 1909. Discussion, p. 141).

Dr. Spence adds that sugars are to be found in quantities in certain barks, and that the physiological importance of these can not be doubted.

The answer would seem to be that whatever occurs in *Ficus elastica* can only be of suggestive value with regard to the guayule. And the behavior of sugar described means that the unused residue of the sugar has been cut out by periderm, just as the unused portion of any other substance may be. But this can not mean that everything which appears in the bark must have been of use to the plant. The statement made by me that the amount of rubber varies from time to time in the year does not mean that the absolute amount in a particular individual is now reduced and now increased. It means that the amount of rubber relative to the weight of the plant is greater at one time than another, and I myself have shown this to be the case. The gradual accumulation in the tissues, unaccompanied by any reduction, of rubber which might serve a storage function, this accumulation following growth, seems to completely contradict the view that rubber is a reserve food. We may very well say that during growth energy is diverted from the secretion, or, as I should prefer to say, excretion, of rubber, and this would accord with the fact that the more energy is expended in growth the slower the secretion takes place.

In the statement to which Dr. Spence refers, when I speak of rubber being cast off in a modified form I do not mean to say that this modification is chemical, or that it takes place before the rubber is cast off, but by virtue of (presumably) oxidizing processes which take place in the cork-cells, which are now dead. This change, it seems to me, can have, in the light of the evidence, no significance to the plant. It remains, however, to show experimentally that my view is correct, but it can scarcely be denied that the evidence against it is tenuous.

#### SUMMARY.

The studies presented in this chapter may be summarized as follows:

1. In the root, rubber is first secreted in the primary canal-cells (plate 41, fig. 6), the activity spreading from this region as a center, but more rapidly along the radius. At about the same time, or, judging from the size of the granules seen, somewhat later, it appears in the innermost cells of the parenchyma rays. Rubber appears in the root earlier than in the stem in the same plant.

2. Accumulation usually takes place in the oldest cells first; that is, those in the outer zones. Thus, in the root the primary cortex contains, before the maximum content for all the cells has been attained, more rubber than the cells of the secondary cortex; and the outer cells of the latter contain more than the inner. Accumulation (in irrigated plants at least) is more rapid in the parenchyma-ray cells than either in the pith or the cortex.

In the primary cortex of the stem rubber may never appear, as, *e.g.*, in irrigated plants in which growth and, hence, secondary changes are so rapid that the primary cortex does not have time enough for secretion.

3. With one exception, namely, in the hypocotyl, the accumulation of rubber in the stem takes place earlier in the pith than in the parenchyma rays or cortex, and earlier in the rays than in the cortex.

At the apex of the stem of field plants more rubber is found in the pith than in the cortex after prolonged drought.

In the hypocotyl (upper zones) accumulation of rubber takes place more rapidly, if not earlier, in the inner parts of the parenchyma rays. This appears to be due to a more primitive physiological condition of the pith of the hypocotyl.

4. With questionable exceptions, the accumulation of rubber is earlier in the "secreting-cells" of the resin-canals than in the surrounding tissues. The exceptions noted were (a) in the apex of a very slowly grown field seedling, in the resin-canals of which no rubber was noted, and (b) in the new twigs, near the apex of field plants. Rubber may be noted, however, in the canal-cells, as in a very rapidly grown irrigated seedling, though it occurs nowhere else.

5. The amount of rubber in the cells of small seedlings<sup>1</sup> in the field is relatively as great, or very nearly so, as in mature plants, except in those seedlings (table 54) which have grown rapidly in the field, and which have not had sufficient time for the accumulation of the full complement of rubber.

6. Rubber occurs unchanged in the portions of the secondary cortex which have been more recently cut out by inner periderm. In the cells arising directly from the outer or inner periderm rubber does not occur. In the bark proper the rubber-bearing tissues alternate with nearly barren suber. Volume for volume, therefore, the bark contains less rubber than the contingent living cortex which still remains unmodified.

7. Rubber occurs in the pseudotylese tissue of the resin-canals in quantities comparable to the amount found in adjacent cells.

8. The accumulation of rubber in the new tissues of secondarily thickened roots and stems is analogous to that in those still in the primary condition. It is for some time absent from the newer parts of the parenchyma rays, and secretion occurs first in the innermost and outermost cells simultaneously. The march of the secretion of rubber is, therefore, from the base toward the tip of new shoots and from the pith and cortex toward the cambium in older stems.

9. In field plants, that is, in those subjected to the usual desert conditions of their habitat, the accumulation of rubber is more rapid than in irrigated plants. The maximum quantity is certainly not reached in four months (June to September, incl., 1908) after growth commences, and it is highly probable that six or more months must elapse.

In a given cell, the amount of rubber in a field plant will generally be greater at the end of one year than in a corresponding cell in the irrigated plant in two years. Also, cells containing a given quantity of rubber will be found nearer the apex of the stem of field plants than of irrigated plants. It is probable, again, that the total amount of rubber that a cell in a field plant is capable of secreting is greater than in an irrigated plant, though this is not certain.

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<sup>1</sup> Chemical analyses of entire small seedlings are misleading, because of (a) the larger relative bulk of the leaves, and (b) the greater relative volume of tissues partially filled with rubber, as in the case of seedlings taken after a period of growth, but before the maximum rubber-content has been reached.



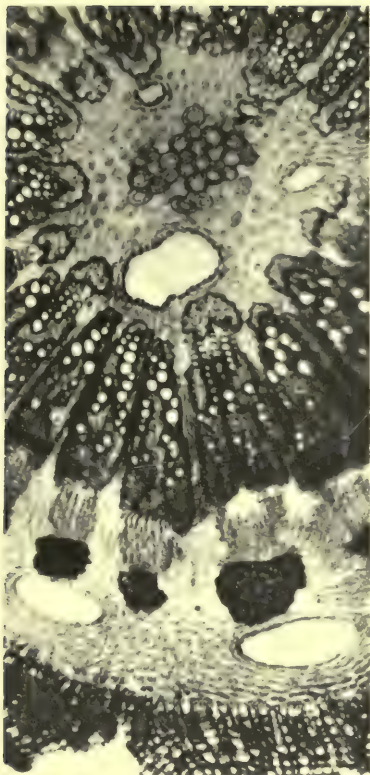
The determination of the time at which the maximum rubber content is reached is of economic importance, as the earlier gathering of shrub involves a considerable economic loss, amounting approximately to the quantity of rubber secreted in one year in the new parts. If consistent, therefore, with other considerations, the gathering of shrub should not occur during, or for some time after the close of, the growing season. It will be understood that by new parts is meant the new tissues within the already secondarily thickened roots and stems, as well as new accretions in length. The time at which the maximum amount of rubber may be expected differs with the length of the growing-season, which depends upon the rainfall and the intensity of the drought following. It thus happens that field conditions are sometimes such as to produce results in field plants (seedlings, table 54) similar to those in irrigated plants.

10. The rate at which rubber is secreted by irrigated plants, under the conditions described for the Cedros experimental plants, is such that at the close of the second season's growth (Sept. 1908), the amount in the cells is sufficient to agglomerate into the large masses characteristic of field plants. This condition was, however, approached after a succeeding drought-period lasting till April 1909 (plate 43, figs. 1 and 2; table 53). In plants grown at Caopas under irrigation, during the first season's growth (1908) and with a restricted amount of water during the second season (1909), the amount of rubber was evidently greater than in the Cedros material<sup>1</sup> and was great enough by October to agglomerate (plate 43, figs. 3, 4), forming dense masses, but not as large as in field plants. There is, however, a large enough rubber-content in such plants for mechanical extraction, though it is probable that some adaptation of the process would be necessary. Although the amount of rubber may be as low as 3 per cent, it must not be forgotten that the rate of growth under irrigation is enormously in excess of that under field conditions.

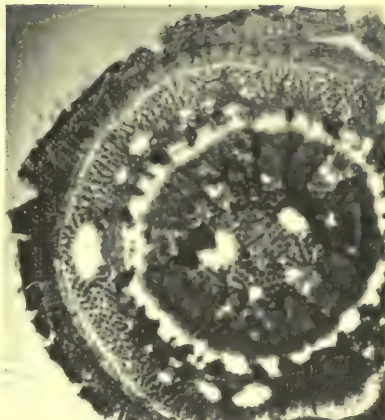
11. There appears to be no direct physiological relation between the secretion of rubber and of resin.

12. Rubber appears to have no physiological function in the guayule plant.

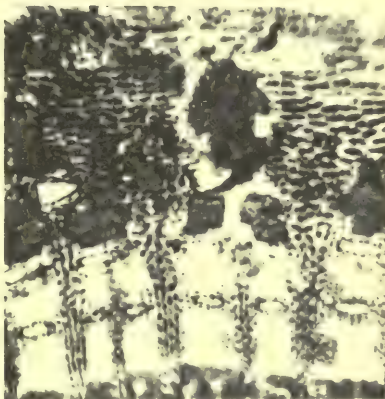
<sup>1</sup> The slowness of secretion in well-watered plants offers an interesting analogy to the behavior of the rubber-bearing latex plant *Castilloa elastica*. (Collins, and Pittier; see Cook, 1903). Olsson-Seffer has also pointed out that the secretion of rubber in this plant is retarded by irrigation, and in consequence it must be deprived of water for some time before it can be tapped to advantage.



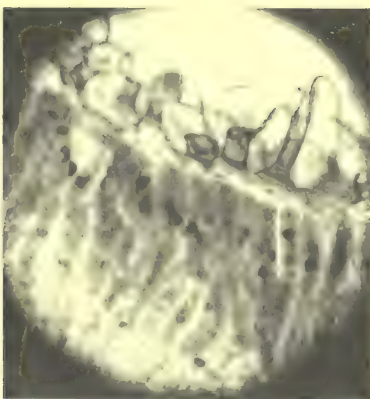
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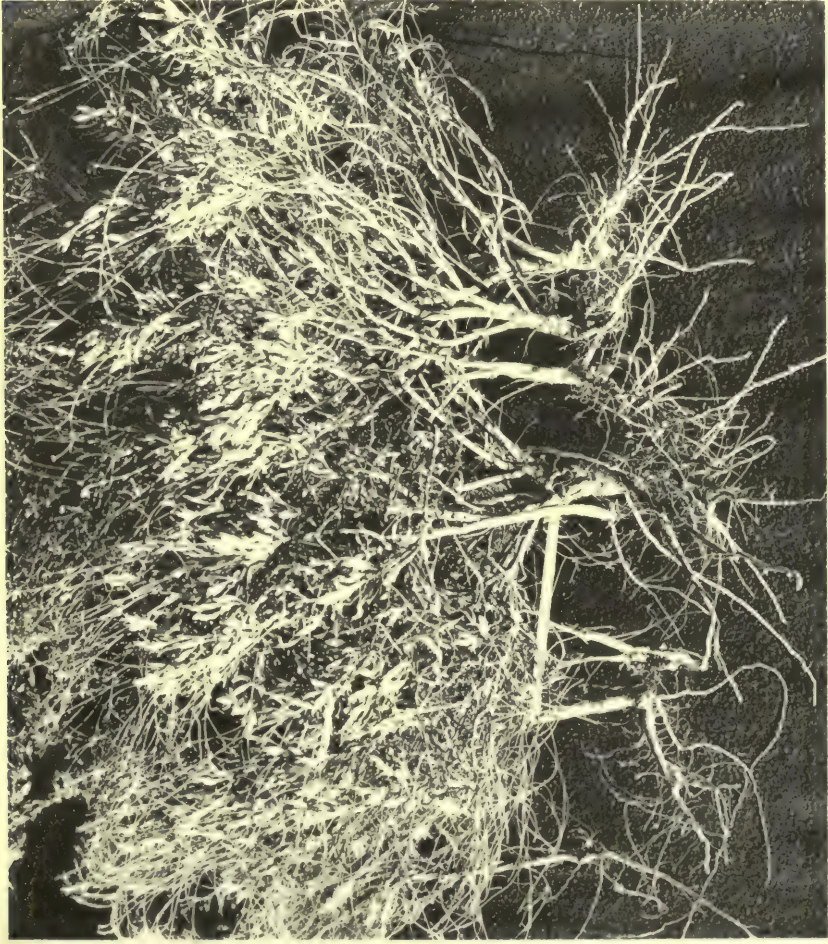


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1. Base of 1908 growth, August. Cedros, irrigated.
2. Growth of 1908 in April 1909. Cedros, irrigated.
3. Cortex, 2-year old stem. October 1909. Caopas, irrigated.
4. Pith of same plant.
5. Epidermis of an old leaf, field plant, April 1909.







A. Irrigated plant, 2 years old. Basal branches which have rooted are spread apart.



B. *Mariola* showing same behavior, normal in this species.



## CHAPTER VIII.

### VEGETATIVE REPRODUCTION.

In attempting to solve the problem of the cultivation of a hitherto totally feral desert plant, it became necessary to determine quantitatively the possibilities of the plant for reproduction vegetatively as well as by seed. As has been mentioned, the percentage of germination is small, even under the best cultural conditions, so that any haphazard field method of sowing seed, in the hope that nature will do the rest, is practically out of the question. In the hope that cuttings could be made to grow readily and in sufficiently large quantities for cultural purposes, this was gone into thoroughly. The net result of all the experiments is to show that only a short zone of the stem is capable of root-regeneration, namely, that immediately above the tap-root, but including some portion, difficult to delimit, of the epicotyledonary region in seedlings and an analogous portion of the stem in retoños (fig. 11). The ability to produce roots in plants from seed is, however, not restricted to the main stem, but, as will be shown, resides also in branches springing from the root-producing zone. This fact is of rather special biological as well as economic interest, and as it throws light on the failure of attempts to grow cuttings I shall first present my observations leading to the conclusion stated.

#### INDUCED ROOT-REGENERATION.<sup>1</sup>

Both the Mexican guayule (*Parthenium argentatum* A. Gray) and its congener, the mariola (*P. incanum* H. B. K.), exhibit methods of vegetative reproduction which, while shared by other plants, are not common to these under the normal conditions of growth. A somewhat detailed account of the matter has already been published,<sup>2</sup> but a brief restatement will be necessary to make clear the point of the present discussion.

The mariola is a low shrub with rather numerous branches rising immediately from the base of the chief stem. These branches arise subsequently to the development of the chief shoot, and not unusually, during the first season of growth, from the seedling. Each following period of development sees new lateral shoots of this kind arise again from the base, either of the main shoot or, secondarily, from an already well-developed basal-lateral shoot. Long continuation of this process results in the dense group of stems arising near the surface of the ground which characterizes the mature plant of the mariola.

It is to be further noted that nearly all of these basal-lateral shoots are provided with their own root-systems (plate 44, fig. B). From the base of each new shoot, soon after it has accomplished a fair amount of development, there spring adventitious roots, one of which, by the direc-

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<sup>1</sup> Presented before Section G of the American Association for the Advancement of Science at the Baltimore meeting, 1908.

<sup>2</sup> Lloyd, 1908b.



tion and amount of growth, becomes, in effect, a tap-root of the branch from which it springs. Subsequent development of roots of the second and higher orders results in the ultimate elaboration of a complete root-system.

We find furthermore that, while the caliber of the basal-lateral stem increases with age, the isthmus of tissue between this and the chief stem increases only slowly, so that there is never more than a weak connection established, and this ultimately becomes disintegrated. In this manner the basal branches in question are set free from the parent stock. There results, therefore, from a single original stock, a group of independent individuals closely crowded together.

A departure from this behavior is sometimes to be found. A glance at the root-system of a single stock will show that the lateral roots run obliquely into the soil, so that they soon attain a considerable depth. From the upper portion of these lateral roots retoños occasionally arise which behave much as do the basal-lateral branches above described, and the net result is the same, namely, to produce a crowded group of individual plants.

The root-system of the guayule, on the other hand, consists of a strong tap-root and several strong laterals, which arise at a short distance below the surface of the soil (plate 9, fig. A). These follow a horizontal path for a distance, it may be, of 2 meters or more from the plant, and constitute a water-collecting system by which the plant derives water from rain-water which does not penetrate deeply—a feature shared by many desert plants (Cannon, 1911). These shallow roots frequently produce root-shoots (retoños) at various distances from the parent stock. I have found them at a meter distant, and it is likely that they may arise still farther away, though I believe less often than at shorter distances.

It may be presumed that shoots, arising, as they not infrequently do, from the basal portion of the main axis, may occasionally strike root as in the mariola. Many thousands of plants, however, have been examined, and only one or two cases have been found which may be permitted this interpretation. We may therefore regard the method described as the only normal method of vegetative reproduction under natural conditions, though it has been observed to occur in the field (Station 5) in two cases in which the aerial portion of the plant had been removed.

On observing for the first time the conditions above described in the mariola, it occurred to me that it ought to be possible to induce the guayule to behave similarly. The fact that a guayule retoño strikes new adventitious roots from its basal zone (fig. 11), and that this, in common with that part of the chief axis above the cotyledons, has a different anatomical structure from other stems, gave color to the notion that there are physiological grounds for entertaining the belief that, with proper treatment, the possibility might be realized.

As experiments to this end would have necessarily involved a long period of time, it was fortunate that I had under observation at Cedros plants which had been growing for the major part of two seasons under irrigation. This was in September 1908. These plants had grown from stumps which were planted in March 1907, by Mr. C. T. Andrews. The

parent plants had been taken from an old stack-ground in Saltillo, at the guayule factory of Martin Brothers, and had started there from seed which had fallen from the stacked guayule. Before being transplanted, they were variously trimmed back, leaving only the lower portions of the main stem and, in some instances, of the lowermost branches. During 1907 the new growths attained a length of about 25 cm., making rounded bushes about 15 cm. in diameter. By September 1908 another 25 cm. of growth brought them to a spread of a meter for the largest plants.

It was then discovered (on the 19th of September) that the lowermost new shoots in certain of these plants had struck root, quite after the manner described for the mariola, and it was further observed that this had not occurred in all of the plants, but either in those plants which had been trimmed back so as to leave only a very short basal portion, or in those new shoots which had arisen close to the tap-root (plate 44, fig. A). In several instances the whole of the lowermost branch was buried by chance in the soil, and in others a part, but neither in these nor in some layering experiments by Dr. Kirkwood<sup>1</sup> was any response observed. The behavior of guayule in this respect is similar to that of certain plants which are subjected to mound-layering. Whether it is possible to compel every plant properly treated to behave in the manner described can not be said, as circumstances prevented a more careful study of the matter.<sup>2</sup> If this should prove the case, it is evident that the branches which are provided with their own root-systems could be removed and transplanted with ease.

### PROPAGATION BY CUTTINGS.

The general conclusion suggested by the above experience was that only cuttings taken from the root, or from a portion of the stem near the top of the tap-root, would succeed, but as the time of my stay at Cedros had drawn to a close it was not possible to direct experiments to test the latter of the alternatives. Table 55, summarizing the results of my study of cuttings, did not include this particular condition, which could hardly have been anticipated. I early found, however, that the stem-cuttings made did not respond, and that recourse must be had to cuttings in which a portion of root-tissue was involved. The scheme of splitting the butt of the plant so as to get two to four pieces was seized upon, the only method of those used which secured positive results aside from pure root-cuttings.

The following conclusions may be drawn from the data in table 55:

1. Cuttings involving stem-tissues alone, with a possible exception of stem-tissue close to the root in seedling or rotoño, do not regenerate roots under the treatment given. It remains theoretically possible, by special and more refined methods, to induce root-regeneration, but for the purposes toward which the experiments were chiefly directed, this is not practicable.

2. Stem-cuttings may be kept alive, after being planted, for a considerable period, particularly during the cooler season, by using careful

<sup>1</sup> Exp. 181, 182, in which either branches or whole plants were layered.

<sup>2</sup> I have noted the same behavior in guayule from Texas planted by me at the Desert Botanical Laboratory and at Auburn, Alabama.

TABLE 55.—*Experiments in propagation by cuttings.*

Exp. No.	Date.	Parts used.	No. of cuttings.	Conditions.	Results.
1-6	1907 Aug. 2	Stem cuttings of various ages.	65	Set vertically or horizontally in trays, watered.	Negative.
7	Aug. 2	Root cuttings 2 to 5 cm. long.	25	Laid horizontally.....	Negative.
8-15	Aug. 3	Various parts of stem.	116	Garden soil, sand and soil, manured soil.	Negative.
16-17	Aug. 3	Root cuttings from rapidly grown plants.	20	Laid horizontally.....	Negative.
83	Oct. 25	Lateral roots of field plants.	2	Laid horizontally, lightly covered with soil (garden soil).	Dec. 3, new shoots 1 to 10 mm. long, on one. Dec. 24, shoots on both. No new roots. Died later.
130a	1908 Jan. 24	Field plants, 1907 growth pinched off, leaves trimmed.	100	Planted in limestone soil in 1-inch paper tubes in tray. Transplanted Apr. 6, into prepared bed of limestone soil, watered and shaded.	Apr. 6, 12 still alive, but all died later. No roots formed.
130b	Jan. 24	Ditto, roots.....	40	Ditto.....	Mar. 3, 2 buds on one cutting. Apr. 6, 9 living, 2 more started after transplanting. Aug. 28, 3 growing well.
130c	Jan. 24	Ditto, 1907 growth cut off and leaves trimmed off.	100	Ditto.....	Apr. 6, 13 alive. All died later, no roots having been formed.
130d	Jan. 24	Ditto, twigs 2 to 3 years old.	40	Ditto.....	Apr. 6, 23 alive, but all died later. No roots.
130e	Jan. 24	Ditto, 1907 growth pinched off and leaves on left.	20	Ditto.....	Apr. 6, all dead. No roots.
130f	Jan. 24	Ditto, cut off obliquely through growth of 1906. Leaves trimmed away.	100	Ditto.....	Apr. 6, 21 alive. All died later. No roots.
131	Jan. 27	Field plants, growth of 1907 broken off; leaves trimmed away.	40	Moist sand.....	Jan. 21, all dying, rotting off.
144	Feb. 9	Twigs 2 to 3 years old, field plants.	10	Water.....	Apr. 25, all dead.
148a	Feb. 24	"Root-shoot" cuttings; lower part of stem and upper part of tap-root, split into 2 to 4 pieces.	31	Prepared bed limestone soil.	Apr. 25, growing vigorously 11, starting 8, well started but wilting, saved by heaping soil about them 2. Started well but died later 1; failed to start 9. May 2, one more started below surface of soil; May 19, another, which later died. Aug. 28, 25 to 32 cm. growth in the above living cuttings.
148b	Feb. 24	Roots.....	2	Ditto.....	Both started, one dying after making 3 cm. growth.
152	Apr. 4	Twigs 3 to 5 years old. Leaves trimmed away.	25	Ditto, with shade of cloth.	Apr. 16, all alive. May 19, 5 budded out. May 25, all appear dead. May 31, one with fresh buds starting. June 15, all dead.
155	Apr. 11	Root-shoot, as in exp. 148, but from small plants.	50	Ditto.....	After a number had made a start (Apr. 25), all died later.

NOTE.—Exp. 1 to 17 were done jointly with Dr. J. E. Kirkwood. These were preliminary, and not under critical conditions.



TABLE 55.—*Experiments in propagation by cuttings*—Continued.

Exp. No.	Date.	Parts used.	No. of cuttings.	Conditions.	Results.
160	1908 May 19	Twigs 20 cm. long ...	356	Planted reversed <sup>1</sup> in a "melga," <sup>2</sup> 2 to 5 cm. projecting above surface of soil.	May 31, 3 started; June 5, 46 started; July 9, 55 started. In some cases buds started 10 cm. below surface. None lived. No roots in any case.
161a	May 19	Twigs 15 cm. long, leaves not removed.	19	Prepared bed of limestone soil. Planted reversed.	May 29, 5 started, but all died later. No roots.
161b	May 19	Ditto, leaves removed.	35	Ditto.....	May 29, 4 started, but all died later. No roots.
162	May 19	Twigs 15 cm. long, foliage trimmed away.	20	Ditto, not reversed...	May 26–June 5, 19 started, all dying later. No roots.
163	May 19	Roots, 2 to 10 mm. diameter.	35	Ditto.....	June 10, 7 started, of which 6 died. One grew well.

<sup>1</sup> On the theory that newer tissues might be able to regenerate roots.

<sup>2</sup> A melga is a bed with a deep border to facilitate irrigation by flooding. Alfalfa is frequently irrigated in this way.

methods. In many instances they will produce new shoots, the size of which varies directly with the volume of the piece. Consequently, examination of the above-ground parts might easily persuade the uninitiated that growth, including that of the roots, had taken place. The fact remains that in no case had the pieces regenerated roots, and in consequence the cuttings all died sooner or later.

3. Root-cuttings may live and become permanently established, but under the conditions used the number was small (plate 20, A1). In these, too, new shoots may be produced without a commensurate growth of new roots, and the cuttings may therefore die after starting.

4. Sectorial cuttings made by splitting the lower part of the plant in such a manner as to involve root and stem tissue grow most readily (plate 20, fig. A, 2 to 4). The pieces heal completely without decaying (fig. 18), and new growths of normal extent under irrigation will be formed, these flowering abundantly the first season. Under favorable conditions about 75 per cent may be expected to live.

5. Stem-tissue may be forced to regenerate roots by planting the basal portions of plants, trimmed close to the top of the tap-root (plate 44, fig. A). Branches which then start out will generally behave as the

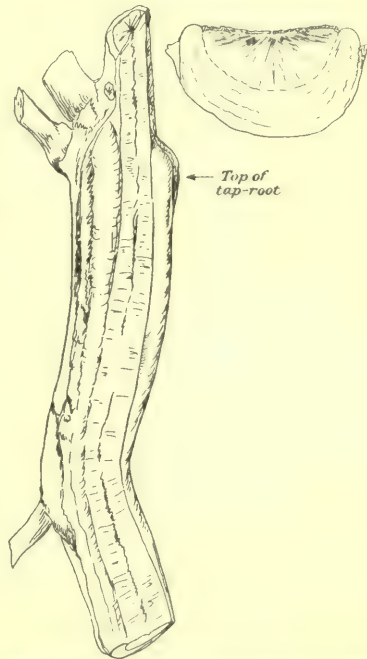


FIG. 18.—A successful sectorial root-stem cutting, showing complete healing.

basal shoots of mariola do normally, namely, each will send out a root from near its base (plate 44, fig. A), which becomes, in effect, a tap-root. Thus these branches become established independently of the parent stock, and may be separated from it and used for propagation. This occurs in nature very exceptionally, but more readily when the top has been removed by design or accident; in the field, however, roots are normally produced from the basal portion of the retoño chief shoot (fig. 11), from which its root-system proper is derived. The more ready production of roots in this manner in irrigated plants is connected with the larger supply of water.

It is seen that the guayule displays a marked polarity analogous to that found in plants which will not regenerate roots from stems when mature, but will do so when young (*Cupressus*, *vide* Goebel, *Organography*, Engl. ed., p. 45, I), and to certain lilies (*Hyacinthus* sp., Goebel, *ibid.*), in which bulbils are formed from the lower portion of a severed stem, but not above. That is to say, the expression of polarity by root-regeneration from the stem is definitely restricted to a particular region of certain stems only, namely, to the lowermost zone of the branches of the second and (probably) higher orders, which themselves arise from a narrow zone of the chief stem just above the tap-root.

Shoot-regeneration is, by contrast, easy, and this is true for the root, from which stem-primordia are absent. It does not appear that external stimulus is necessary, for wounding the cortex of the root *in situ* is not followed, in any of my experiments, by shoot-formation at the point of wounding. Nevertheless, as in many plants, a complete severance of a root left *in situ* is frequently followed by shoot-formation, but in a position determined by other conditions, such as dying back, resulting from drought. Thus it appears that the notion formulated by Miss Kupfer (1907), that the disposition to form roots is much more generalized than to form shoots, does not include cases like this before us, which need elucidation as much as any. And as McCallum (1905) has well said, the problem of regeneration is more especially to determine the cause of non-development "of parts" in the normal life of the plant.

## CHAPTER IX.

### THE CULTIVATION OF GUAYULE.

Under the cultivation of guayule must be included all operations intended to modify the relation of the plant to its environment. These operations may be forestal or cultural, in the narrower sense. It is the purpose of this chapter to set forth the conclusions as to the possibilities which have presented themselves in both these directions. Although only a beginning has been made in the solution of the many difficult practical problems which have arisen, the more immediately insistent questions involved have been fairly if not completely answered. The difficulty of practice is not lessened by the fact that the problem before us is distinctly a desert one, and the final answer to many questions may not be obtained for many years.

#### FORESTAL OPERATIONS.

##### PRESENT FIELD OPERATIONS.

Up to the present time, with only very few experimental exceptions, field operations have been confined to the collection of shrub in the greatest possible amount with the greatest ease, for the sake of the immediate monetary return. This has had both a bad and, in less degree, a good result. In many places where shrub had been taken there were so many small plants that it was thought that it would not pay to collect them, and these will serve to repopulate the areas so treated. In other places, where the stand consisted only of large plants, nearly every vestige has been removed, leaving at most only the occasional small plants to lay the foundations for the future. If in such places a few healthy medium-sized plants had been left to produce seed, as common sense should have dictated, ground that will be barren of guayule for many years might have been repopulated, at any rate to some extent.

The method which has ordinarily been used is to pull up the plant by hand, and, while the method of cutting it off at the surface of the ground has been advocated and to some extent practiced, pulling has been most largely used. But in very rocky areas, where the plants frequently grow in the fissures of the rock, from which it is often impossible to pull them out, the peons will break or twist off the top, leaving the butt in the ground. A specific case of this kind was noted by me in a part of the Sierra de Ramirez, a range of mountains lying partly in each of the States of Zacatecas and Durango, opposite Tanque de la Pendencia. On first entering the guayule area, which had been worked in the winter of 1907-08, scarcely any guayule was to be seen, but further search discovered numerous young growths, visible with difficulty on account of their color when seen in April 1909, which had come up from the basal portions of plants which had been twisted off. Bare as this ground appeared to be of guayule, there is little doubt that in time the stand will be replenished to a large degree, if not fully.



In the Lomerio de Zorrillos, some leagues further south, where the substratum is made up of fine limestone soil containing stones of various sizes, it is easy to pull the plants up, and here all the larger ones were taken. As the number of small plants was, however, very great, all these were left, and number 600 to 800 to the 100 square meters, weighing 1 to 2 tons to the hectare. This condition probably represents the best that may occur under the old methods, and is but seldom found. In many spots from which larger plants had been taken, pieces of root left by breaking off were found to have produced retoños.

The work of pulling up the guayule is done by peons who tie the shrub into bundles, make up burro-loads, and take it to a neighboring "campo de guayule," a field-center of operations, where the shrub is baled in hand-presses. From here it is hauled in wagons to the most accessible shipping-point on the railroad, and so by rail to the factory.

In undertaking to harvest the shrub from a particular region, the usual method is to let a contract to local agents who can command the conditions, which, as may well be imagined, are often severe on account of the great distances and lack of water. The easiest time to work is while the ground is still soft from the rains and when water is relatively plentiful, and it happens that this is the worst possible time to take the plant as regards its rubber-content. At that time also the shrinkage in weight is much greater, both by the loss of a greater amount of water in the plant and the larger bulk of the foliage.

#### SUGGESTED RULES OF PRACTICE.

The statement will not need defense that an immediate desideratum is a rationale of forestal operation, in order that the present field supply, already much reduced from the original stand, may be kept from being well-nigh wiped out. The data upon which rules of procedure must be based, in the absence of still necessary extensive quantitative study of treated areas, have been presented in Chapter IV. The general practice indicated by the experiments recorded will therefore be stated here.

1. Guayule should be gathered by cutting it off at the level of the ground. That which is allowed to project above the surface will die back more or less and be an economic loss, as these parts represent a substantial proportion of the weight of the plants. The cutting should be done with a sharp grubbing-hoe (*talacho*), a method which is easier on the men, as well as contributing to the preservation of the stand of plants. It is practically certain that new shoots will arise from many of the parts left in the ground, and these, during the first season, will produce flowers, the seeds from which will help to repopulate the area.

It has recently been suggested by Escobar (1910) that, after cutting, a shallow depression be cut in the soil about the remaining root, for the purpose of catching the run-off, thus increasing the water-supply. Further operations (terracing or furrowing along the contour lines), designed to hold back the run-off, are also recommended. In many situations it would be difficult to carry out schemes of this kind.

2. Only plants 40 cm. or more in height should be taken on the first cutting. Five years later there should normally be a crop of 40 cm. plants,

which may then be taken. Between 30 and 40 cm. the maximum economic efficiency of growth obtains, and this lies between 10 and 15 years of age. Fifteen years is therefore the rotation period, but as the growth efficiency of a plant falls after this age has been reached, these plants must be removed each fifth year. The advantage of this rule is to be expected not only in the growth of the plants already there, but also in the great efficiency of seeding. The question has been raised as to the possible increase of efficiency of germination by partial or total clearing of the land, thus removing the factor of competition.

3. Removal of the vegetation other than guayule. It is too early to make any definite statements as to the value, even with regard to the well-being of the mature plant, of clearing operations on guayule lands. The experiments which have been initiated involve an area of about 75 acres, which were well cleared of all vegetation excepting the guayule, the "palms" (*palma samandoca*) which produce fiber, and the few cacti, of large species, which occupy little area and do not constitute an aggressive element in the vegetation. The clearing of the land has the effect of loosening the more superficial layers of soil generally, and to some depth in spots. On general grounds this ought (1) to remove competition with other plants, which, as has been shown elsewhere, is not insignificant and frequently constitutes a real menace to the guayule, necessitating partial clearing, at least. This competition of course relates especially to the water-content of the soil. Unless the removal of the covering allows greater washing than in any event occurs, it should render more water available for the guayule and thus enhance growth. It must not be forgotten, however, that a much greater growth is correlated with reduced activity in secretion of rubber, either directly or by reducing the volume of the rubber-bearing tissues, as has been brought out in the discussion of plants under irrigation and from areas of greater rainfall (Chapter V). (2) It is important also to know what effect the removal of the vegetation has upon the crop of seedlings. The evidence so far obtained appears to favor the clearing of the land. I refer especially to the census of seedlings made at Station 2 (page 70), in which are recorded numbers of seedlings far in advance of those found elsewhere. As to the question of protection afforded young seedlings by the shade of other plants, of no small importance in many cases, as has been repeatedly indicated by studies at the Desert Botanical Laboratory, it may be concluded that the number of seedlings which survive a six months' drought, as observed by myself in April 1909, is sufficient to warrant the statement that not enough succumb to unfavorable conditions to neutralize the good effects, as seen in the surviving numbers. It seems probable, therefore, that clearing the land of other vegetation, saving the species above mentioned, is, on the whole, beneficial to the guayule.

As to the specific question of the response in growth, all that can be said at this time is guesswork. The areas which were cleared, as it happened, were subject to severe droughts from the time of clearing in the winter of 1907-08 till the summer of 1909. It is hoped that the abundant rainfall of the season now drawing to a close will enable us to form some conclusion on this point.

## HARVESTING PERIOD.

The question of the variation in the relative rubber-content of the guayule according to the time of the year is undoubtedly of more importance than is at present appreciated. The loss arising from this cause, moreover, can not be detected by the chemical control of a factory laboratory, for the reason that the new succulent growths when dried add but little to the weight of the plant, while their capacity for rubber-secretion is indicated by their living volume. The "shrinkage" between field and factory referred to by the manufacturer is equally inefficient as an indicator of the loss, in a practical sense; shrinkage consists of all kinds of loss in handling and transportation from the field to the factory, an important economic factor which, while including the loss under consideration, leaves it undiscoverable.

An element of uncertainty arises from the different moisture-content of the shrub at various seasons. Thus, the shrinkage in weight from drying in field plants is from 20 to 25 per cent (exactly in my determinations between 22 and 23 per cent) during drought; in irrigated plants it is as high as 50 per cent. In August 1908, at the height of the growing-season, the water-content ranged between 25 and 50 per cent, averaging in the neighborhood of 35 to 40 per cent, as high, nearly, as in irrigated plants, in which it rarely falls below 40 per cent, and is usually about 50 per cent. In addition to this, the weight of the additional leaves in summer is not negligible. I shall therefore venture to state with some insistence that, assuming normal distribution of rainfall, the gathering of shrub during summer months and for several months thereafter can mean, practically, only the total loss of the rubber accretion of a whole year. The small amounts of rubber undoubtedly present in the newer growths can scarcely be recovered by mechanical means, while the ready breakage of the slender and weak twigs of recent growth would in any event result in a loss.

Another consideration is involved also. The germination during the growing-season results in the annual crop of young seedlings, the greater part of which, on account of the numbers and small size, would undoubtedly be destroyed by the peons at work collecting shrub. Aside from this, the peons should be not only instructed but compelled to work carefully, so as not to destroy the small plants.

## RESEEDING BARREN GROUND.

Land from which guayule has been completely removed may, under favorable conditions, be restocked by the simple operation of reseeding. Whether the cost of doing this would be justified, however, is doubtful, since an area of any size would require an immense amount of seed, which at present it is difficult to obtain in quantities, and since the percentage of germination under natural conditions would be very small.

Whether the business view will see a sufficient monetary recompense in the returns from following the procedure above recommended is not the present problem. Local conditions vary too much to solve it in general terms. This much, however, may be said: that the rules of operation outlined are dependable in the degree indicated, and that the disregard of them, or of some equally or more efficient ones, will only lead to the practical extermination of the plant.



### CULTURAL OPERATIONS.

Although it will be granted that forestal operations are of immediate and great importance for the preservation of the natural stand as a source of revenue for as long a period as possible, the ultimate and adequate solution of the production of guayule shrub lies in its successful cultivation. That this is possible seems at the present not to be overstating the case. The abundant and ready growth of guayule under irrigation, its drought-resistant qualities, its consequent adaptability to comparatively meager irrigation, if this condition is imposed, and its ability to secrete rubber, though in relatively smaller quantities per unit-volume of tissue, under irrigation properly alternated with drought, are established facts. It remains, therefore, to test, on a larger scale than has hitherto been attempted, what may be done to establish the culture of the plant on an economic basis. But in stating the positive basis for success the difficulties must not be underestimated. These will be indicated in what follows, and it will suffice here to point out, in a word, that the great difficulty lies in the initial work of establishing the plants, which necessitates water. It would be useless to attempt cultural operations without it.

#### SEED.

Should it turn out finally that the raising and the transplanting of seedlings is a desirable method of procedure, the obtaining of a sufficient amount of seed will be an important desideratum. At present it would be necessary to collect seed from the field. This is costly and uncertain. Experience has shown that the ripening of seed in the field is uneven; much of it quickly falls off, and the most satisfactory places to collect are frequently far removed from habitations. Hand-picking is slow, but could be rendered more efficient by the arrangement of a device of wire and cloth, in two pieces, to be held under the shrub, from which the seed could then be dislodged by light beating. It seems, however, unlikely that any field method of collecting seed will be as satisfactory as its production by irrigated plants, which, in the climate of North Zacatecas, will ripen seed for the greater part of the year. The ripening of a large amount at one time will render rapid collection easier. Some such device as suggested will in any event be necessary, as the seed must be collected and submitted to optimum conditions in order to get the maximum germination. It has been found that the ordinary conditions of growth, even under irrigation, are not efficient for this result. The advantage of growing plants under irrigation is in the convenience and economy in obtaining seed, and not in its superior quality. Kirkwood (1910a) found that the number of good seed from irrigated plants does not exceed 17 per cent, and this is sometimes, but not often, surpassed in field plants.

#### THE RAISING OF SEEDLINGS.

The small size of the seedlings and their tender character when young make it necessary to handle them with considerable care. The precise conditions for their successful culture have been studied by Dr. Kirkwood (1910a) and by myself, and from these experiences, but more particularly from my own, the following practical suggestions are made:

The probable necessity of transplanting large numbers of seedlings at a very great risk of loss led me to adopt experimentally a scheme used in the tropics, where the hollow joints of bamboo are used as flowerpots in which to raise cacao, coffee, and other seedlings. When ready for planting in the grove the whole pot is planted, and the decay of this, aided by fracture, sets the roots free without any disturbance. In a preliminary way the joints of "carrizos" (*Arundo donax*) were tried, but proved too small. Combining this idea with that of the paper flowerpot, a unit system of wooden trays and paper tubes was devised,<sup>1</sup> the tubes being 1 square inch in transverse section and 6 inches long (plate 45, fig. A). As trials with these taught that they afforded too little room for the horizontal development of roots, a comparative test with similar tubes of 4 square inches transverse section was carried out under identical conditions. A tray 20 by 28 inches inside measure and 6 inches deep was filled with these tubes (plate 45, fig. B), the whole being filled with unsifted limestone soil in which there were a great many small fragments of caliche and stones. The tray was placed in a melga and watered by subirrigation. The surface was shaded at a height of 4 cm. by a thin cotton cloth supported in a frame. The shade was raised or lowered as the surface appeared to need more or less air, so as to check the growth of fungi (a *Coprinus* sp. was very frequent in the decaying paper of the tubes), among which one species, at least, caused damping-off. On February 16, 1908, 1.5 ounces of seed were sown. The germinations were as shown in table 56.

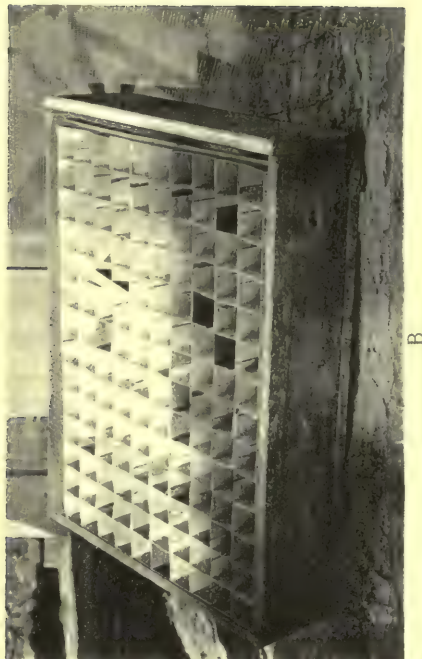
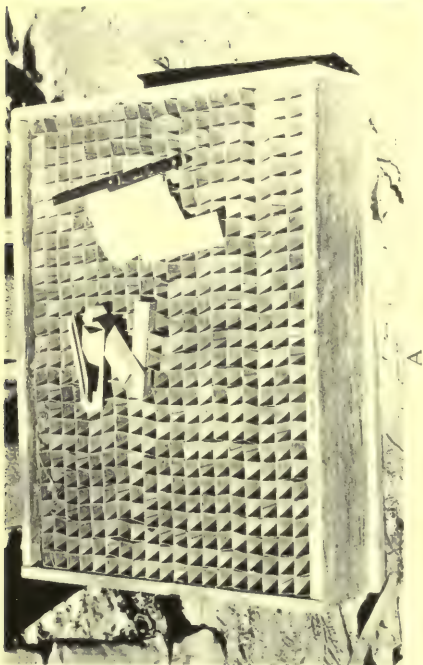
TABLE 56.

Date.	Germinations for period.	Total germinations.	Loss.	Net total living seedlings.
Feb. 26 .....	2	■	..	2
27 .....	2	4	..	4
28 .....	18	22	..	22
29 .....	50	72	..	72
30 .....	32	104	..	..
Mar. 8 .....	300	404	..	..
12 .....	100	504	..	..
16 .....	21	525	41	484

The appearance of these seedlings is shown in plate 45, figs. C, D, from which it will be seen that a good, fairly even stand of sturdy seedlings (plate 46, fig. A) was obtained. The size of the tubes used was, of course, a compromise, but fig. 19, A, shows that a sufficiently satisfactory root-system can grow in them, though of course by no means as good as when the roots have normal freedom (fig. 19, B), which in any case is neither desirable for practical purposes nor expected. The tray held 140 tubes, from which it is seen that there was an average of about 3 seedlings to the tube. The unevenness was due to the removal of seed from its original position by rain or occasional surface-watering, which is desirable to aid in preventing too rapid caking of the surface. To prevent this movement of seed the surface should be as level as possible. The margin of the tray

<sup>1</sup> By Capt. L. C. Andrews.





A. Flat filled with paper tubes, one square inch in transverse-section.  
C. Exp. 141(3), 1-inch tubes; very poor growth. Exp. 143, 4-inch tubes.

B. Flat with 4-square inch tubes.  
D. The same, seedlings well grown.





should preferably be somewhat higher than the surface of the soil, as this, in addition to enabling one to manage the shade better, prevents the drying out of the soil near the edge, in consequence of which the germination is not so good.

The subirrigation may be managed best by placing the trays in melgas of a depth sufficient to bring the surface of the water to the level of the top of the soil in the tray. In order that the water may gain free access to the soil the sides of the trays must be provided with a number of holes.

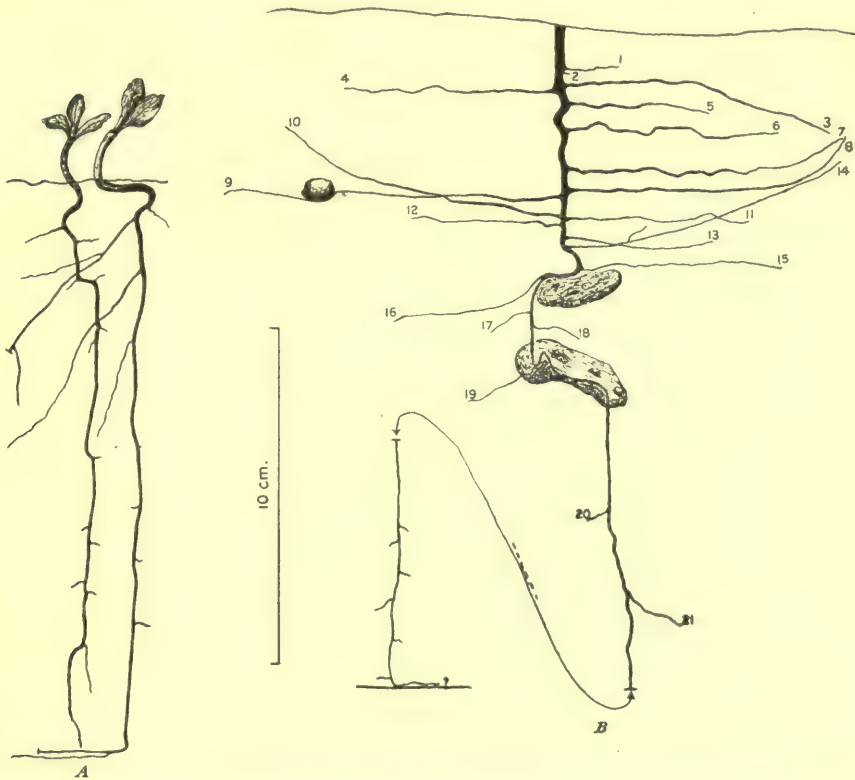


FIG. 19.—A, the roots of two seedlings grown in 4-square-inch paper tubes; B, a root-system of about the same age, growing in a box. X9/20.

Despite the apparent indifference of guayule seed to the temperatures recorded by Kirkwood (1910a), seeds germinate more promptly and, what is more important, the seedlings make a much more rapid growth during the summer months, as my experiments in July and August 1908 showed. In winter, also, the seedlings were frequently killed in part by frost, in part by a storm of hail, and were more subject to damping-off. The heavy rains of summer also prove more or less destructive, and it was found that the seedlings with the shortest hypocotyls survived the best. For this reason as thin a shade as possible is desirable, the object of this being to preserve the superficial soil-moisture and to cut down the light as little as possible.

When it is desired to transplant the seedlings, the tubes will be found to be soft and partially decayed, so that they may be torn by slight pressure when being placed in the ground. This will favor a prompt adjustment to the new conditions. The loss will vary and can not be foretold,

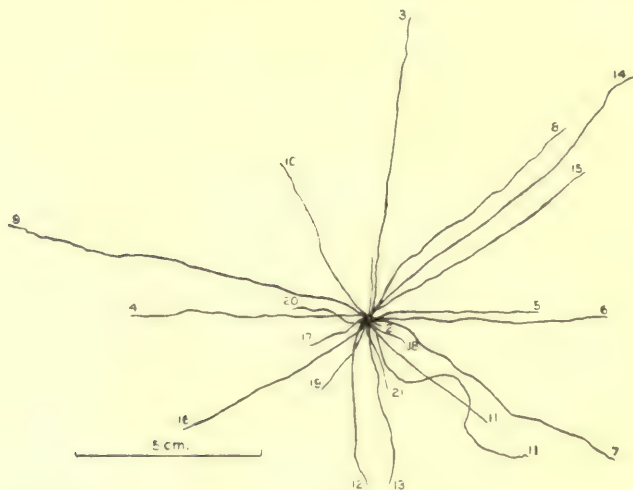


FIG. 20.—The same root-system as shown in fig. 19, B, projected on a horizontal plane.

but with care should be small. As time did not permit an extended trial of this, however, I am unable to state economically valuable results, though some indication has been had from the following:

*Experiment 79.*—Of 449 seedlings (small plants 1 to 5 years old), transplanted into irrigated ground by a peon, 300 lived. The transplanting was done Nov. 26, 1907, care being taken to prevent the roots from drying out, and the ground was well irrigated. On Feb. 16, 1908, the first indications of growth were seen, but the plants started unevenly, some not showing signs of new growth until Apr. 9.

*Experiment 159.*—May 3, 1908, 5 seedlings were transplanted in 1-inch tubes, the upper 5 cm. of the tube only being preserved. All lived and grew well till last observed, Sept. 1908.

*Experiment 153.*—Apr. 8, 1908. Of 14 small seedlings (epicotyl 10 mm. long in the largest) transplanted into a prepared bed, 12 grew well, 2 died.

*Experiment 164* (J. E. Kirkwood).—On May 13 a bed was prepared by digging up the soil and flooding to a depth of 4 inches. On the following day 1-square-inch paper tubes containing seedlings an inch high were set in the wet ground their full length. These plants had been grown in the tubes from seed and were some two months old. 64 of these were planted, and nearly all lived.

*Experiment 165* (J. E. Kirkwood).—50 tubes containing plants of the same lot as the preceding were set in relatively dry soil which showed visible moisture an inch or so below the surface. This was done May 14 and the ground received water to saturate several inches on the 18th and 19th. A few of these survived.



*Experiment 166* (J. E. Kirkwood).—Bed prepared as above and covered with 4 inches of water. On the following day 250 plants (seedlings) of three months or less were transplanted into this bed. These plants received no more water than what was given at the start, in order to test this practice in the transplanting. In five days these plants appeared to be dead.

*Experiment 167* (J. E. Kirkwood).—Bed prepared as before and watered to saturation. Into this 15 young plants were set on May 15 and immediately watered by flooding. The bed was watered again on May 16. Nearly all of these lived. It resulted that in 164 and 167, in which abundant watering was had at the start, nearly all of the plants lived. In the others nearly all failed.

Transplanting cultivated seedlings into the natural habitat was tried, but the plants were destroyed by goats. The operation is fraught with much difficulty on account of the character of the ground, and would not justify itself practically.

It may properly be said that the raising of guayule seedlings, more particularly during the first few weeks, is not a mere rule-of-thumb procedure. One has to watch them with care and learn their idiosyncrasies. Later they become quite resistant and may be handled much more easily.

The best soil for them, so far as experiments by Kirkwood (1910a) and myself have shown, is the limestone soil of their natural habitat (plate 16). Soil which contains a good deal of humus appears unfavorable for young seedlings, as, among other difficulties, damping-off is very prevalent. However, they were found to have germinated abundantly after lying in such soil for seven months, and grew well, though it must not be forgotten that the soil must have suffered considerable change by leaching and chemical action in the interval. The action of fertilizers has not been tried as yet either on seedlings or mature plants. Recent experiments have, however, shown that guayule will grow well in a noncalcareous soil, and respond readily to sodium nitrate.

The presence of small stones in the soil appears on the whole to be an advantage. The following experiments were done to test this point:

*Experiment 138*, Jan. 24, 1908.—Into three root-cages with sloping glass sides three lots of seedlings of about equal size were transplanted. One (I) of these contained very finely sifted limestone soil; the second (II), similar soil mixed half and half with fine angular gravel of limestone; the third (III) was filled with the same fine soil and coarse gravel (1 cm. ave. diam.), the gravel occupying the space that it would without the soil. Feb. 22, length of tap-root in (I) 50 mm.; (II) 50 to 60 mm.; (III) 60 to 120 mm. These measurements represent differences in rate of growth of the tap-root, which was about the same length in all at the beginning of the experiment.

April 5, the individual measurements of the roots were as follows:

(I) 10, 10, 10, 10, 12.5, 14, 17 cm. Average, 11.9 cm.

(II) 20, 17, 16, 13, 14, 15 cm. Average, 15.8 cm.

(III) 30, 31, 26, 23, 26, 17, 14, 14, 20, 25 cm. Average, 22.6 cm. These differences were reflected in the aerial development, those of III being obviously in advance of the others.

*Experiment 139a.*—Two seedlings of nearly equal size were planted January 24, 1908, in a 5-gallon oil-can, half of which contained a soil made up of coarse gravel and fine soil (of the latter only so much as would go between the gravel), while the other half contained uniform, finely-sifted soil of the same kind. The watering was equal for both sides, and sufficient to keep an abundance of water available. The subsequent growth in the plant in gravelly soil was very much more marked, as shown in the left-hand plant on plates 18 to 20, the limit of growth for the year being nearly reached in four months. This plant, which weighed 8 ounces, produced fully 2,000 seeds. The development of roots was correspondingly greater in the gravelly soil, and careful removal of the roots showed that they were confined chiefly to this soil, though occasional roots of each plant reached over into the territory of the other. However, it should be noted that there appeared to be a tendency of the roots in gravelly soil to grow toward the fine soil, as seen in plate 20, fig. A, in which the plants are oriented with respect to each other as they grew. In these experiments, therefore, the gravelly soil was more favorable to root-development, a result which appears to harmonize with agricultural practice.

#### IRRIGATION.

If large numbers of seedlings are to be raised, the method of watering will introduce a material element of expense, aside from the cost of the water. Hand-watering of the surface would prove to be laborious and expensive. For this reason a method of subirrigation was tried, with the results as stated above. Additional evidence is as follows:

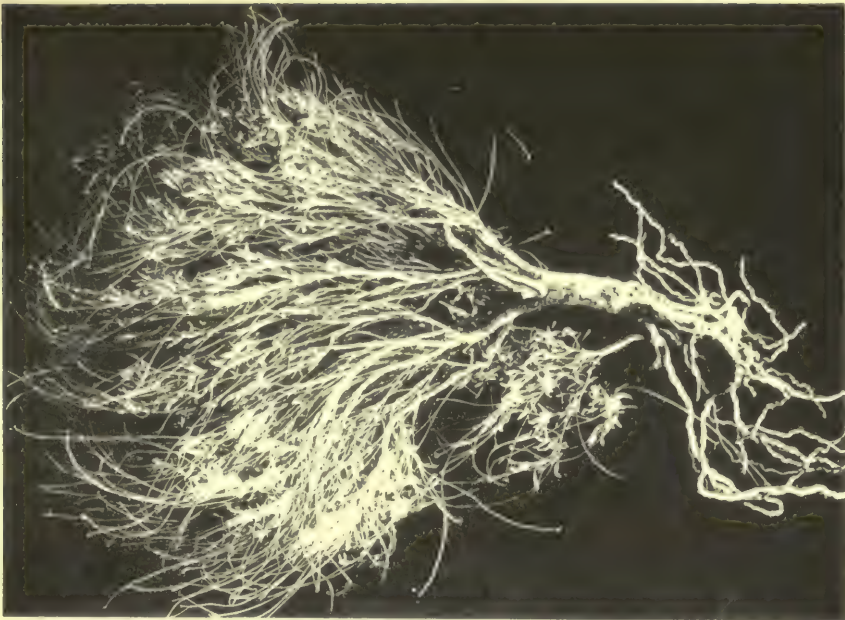
*Experiment 141.*—To test the relative value of subirrigation, with and without shade, as compared with surface watering. Four trays with 1-inch paper tubes (plate 45, fig. A) were filled with limestone soil mixed with gravel, each sown with 1 ounce of seed.

- (I) Placed on the surface of the ground and shaded by a thin white muslin screen.
- (II) The same, but without shade.
- (III) Placed in a melga, and shaded as above.
- (IV) The same as III, without shade.

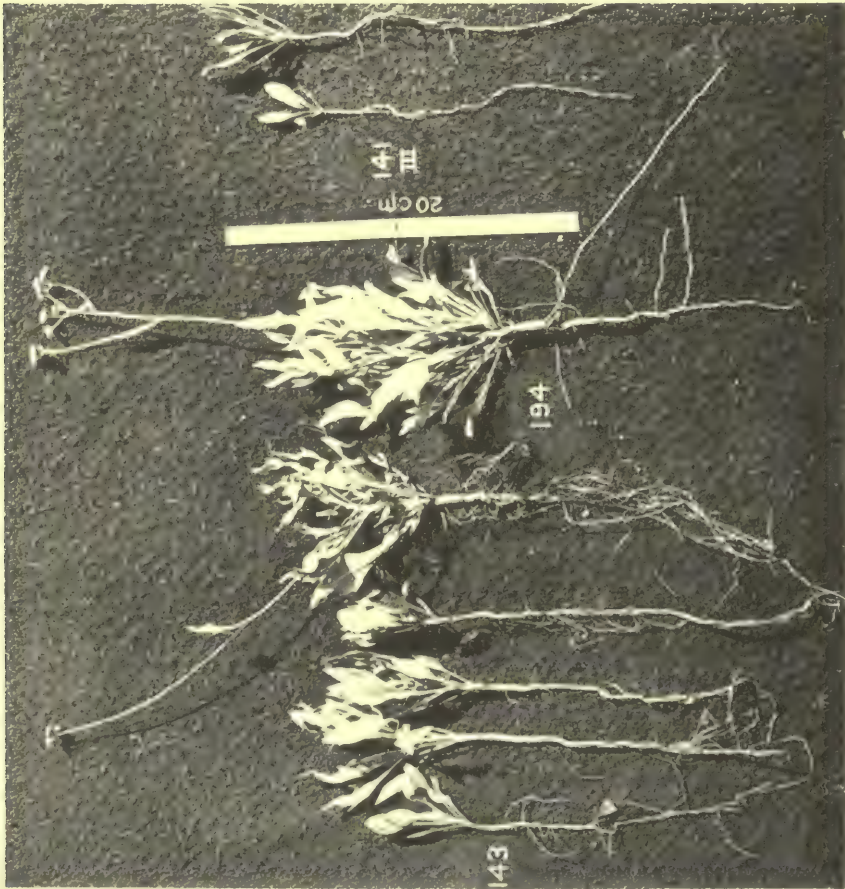
III and IV were watered by subirrigation; I and II by surface watering, and served as a check on III and IV. It was noted that it was very difficult to keep II wet enough. The surface of IV was never dry.

In both shaded trays the germination was far in excess of that in the control. In both the subirrigated trays taken together, the germination was over twice that in the surface-watered trays, though it was slightly more in the shaded, surface-watered tray than in the unshaded, subirrigated tray. The result indicates clearly that subirrigation with shade is the most favorable of the four conditions. It should be noted that tray III was left unshaded after February 13, in order to avoid extreme etiolation, and this may have lowered the subsequent rate of germination without vitiating the general result.





B. Irrigated plant (Caopas) with a retazo.



A. Seedlings from experiments indicated.





TABLE 57.

Date of count.	Numbers of seedlings in—			
	Tray I.	Tray II.	Tray III.	Tray IV.
Feb. 7 .....	6	5	18	9
8 .....	12	0	34	6
9 .....	20	2	42	3
10 .....	21	12	58	25
11 .....	28	11	40	10
12 .....	16	3	25	11
13 .....	6	3	13	4
14 .....	8	7	8	3
17 .....	15	2	15	4
19 .....	3	0	5	15
22 .....	6	2	12	9
24 .....	5	0	0	12
Mar. 16 .....	21	19	8	51
Totals .....	170	57	283	184
Less loss to Mar. 16 ..	13	38	35	40
Total alive .....	157	19	248	144

## TRANSPLANTING.

Another method of getting a stand of guayule started and having the advantage of speed is by transplanting field plants into irrigated ground. Experience has taught that it is of little use to attempt to preserve the aerial part of plants of any size, and that even small ones frequently die back. Of a plantation of some hundreds of individuals so treated (at Caopas), scarcely 25 per cent grew, but upon cutting them back a considerable additional number revived (plate 46, fig. B). If it should be found desirable for any reason to start a crop of guayule from field plants, the best method is to cut back to the top of the tap-root and send the tops to the factory for extraction. The returns from these would go far toward the expense of the operations. It is difficult in any event to start stocks unless previously pollarded.

The portions to be planted should be handled as rapidly as possible, being kept from drying out by means of wet burlaps, or some such means. They should be planted deeply, the cut surface being no higher than the surface of the soil, and they should then be thoroughly irrigated. The question as to the amount of water which may be used without doing them damage is answered by the simple experiment (exp. 145, Feb. 9, 1908) of putting a number of plants into water with their roots and basal part of the stem totally submersed. In four days numerous actively growing lenticels were to be seen on the submersed stem, and on March 14 a rootlet 10 mm. long had grown from one plant, while others had started. By February 24 rootlets 6 to 8 mm. long occurred on the upper parts of the tap-root, and even roots of the third order were subsequently formed. There was no sign of disorganization, so that, unless the soil itself should introduce unfavorable elements, we may believe, as indeed experience in general shows, that the guayule can stand abundant water.

The best time of the year for transplanting, as shown by the prompter responses of the experiments cited in Chapter VI, is in late spring and in summer, when the warmer night-temperatures aid in stimulation. The differences in this regard were very noticeable and showed conclusively that winter, in North Zacatecas at any rate, is unfavorable for cultural operations of any kind.

The advantage of cutting back to the region of the tap-root, in addition to avoiding the loss from dying back, is to be had in the behavior which I have described at some length in Chapter VI, namely, the production of basal shoots which root independently. These shoots will be produced the more frequently the nearer the tap-root the cut is made. As also the guayule frequently sends out new shoots before any new roots have been formed, there is less likelihood that these will exhaust the available moisture when the whole of the transplanted portion is covered with soil.

#### HARVESTING CULTIVATED GUAYULE.

It is almost gratuitous to say anything about this topic, as up to the present time the facts have not warranted cultural trials on a scale sufficient to make available a crop of anything but limited experimental size. We are justified, however, in drawing a few conclusions from the facts which have been brought to light in the present paper.

Assuming that the amount of rubber ultimately produced by guayule under irrigation is sufficient to warrant its culture, it seems clear that the methods of harvesting should be approximately as follows: The new growths, say of two years, of plants about a meter in spread,<sup>1</sup> may with advantage be removed by a cutting instrument, so as to leave the butt undisturbed to shoot out afresh. The branches which have rooted can then be removed by hand simply by breaking them away, and replanted. These are usually supplied with a strong root which can be pulled up without severe damage. In this way the cultivated stand may be increased *ad libitum*, provided areas with sufficient water are at hand.

#### CATCH CROPS.

Immense areas of land are available in the Mesa Central of Mexico, and doubtless elsewhere, where "riego temporal" is practiced. This system of irrigation consists of ditches to catch the run-off, leading it to the fields. The behavior of guayule would seem to justify the belief that this plant could be grown for a sufficient period, say two or three years, in such irrigable areas, and the expense, in part at any rate, offset by growing corn or some other suitable plant, as a catch crop. The guayule, when of sufficient size, should then be "laid by" to endure a period of drought till it becomes usable, when it could be cut as suggested, and restarted. This suggestion, and it is that and no more, deserves a serious trial.

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<sup>1</sup> Assuming the conditions which have constantly been referred to in this work.



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NOTE.—A few of the above citations have been introduced during proof reading for the sake of completeness.

















Botany.

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Author Lloyd, E. E.

Title Guayule (a rubber-plant of the Chihuahuan desert)

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